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Does natural foraging niche influence captive animal health and welfare?

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Abstract

Understanding the basis for differences in how species typically respond to captivity is fundamental for addressing welfare-relevant management problems created by captivity. This can be achieved by formal cross-species comparisons and testing hypotheses for how species-typical ecology and biology might affect their representatives' typical captive response. My PhD examined potential foraging-niche related risk factors, i.e. the way a species uses its habitat and resources in relation to gaining food, for two different types of welfare-relevant management problem across three taxonomic groups. Using phylogenetic comparative methods to control for species non-independence due to shared ancestry, I examined relationships between hunting behaviour and route-tracing severity across zoo-housed Carnivora; and determined whether wild food-search or -handling behaviours predict the prevalence of feather-damaging behaviour and other stereotypic behaviour in pet Psittaciformes. Across zoo-housed Lemuriformes, foraging niche was just one of three aspects of species-typical biology assessed for potential predictive effects on a second type of management problem: susceptibility to weight gain. Taking an epidemiological approach, I also explored several individual-level potential demographic and environmental risk factors for susceptibility to weight gain across a subset of four Lemuriform species. Naturally relying on extensive food-handling was revealed as risk factor for feather-damaging behaviour across Psittaciformes, and adaptations to unpredictable wild food resources might be a risk factor for weight gain in Lemuriformes. Regarding the latter, epidemiological analyses revealed several demographic risk factors and one environmental one in male lemurs (being housed with only fixed climbing structures). Based on my results, I make practical recommendations to help address these specific management problems; describe fundamental, collection-management benefits this approach yields, by identifying types of species less-suited to captivity; and detail areas for future research, with the overall aim of improving wellbeing of thousands of animals across many species.

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Author’s declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's *Regulations and Code of Practice for Research Degree Programmes* and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

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Chapter 1: General introduction

1.1 Background

Humans have kept wild animals in captivity for thousands of years. Genetic and archaeological evidence suggests that around 12,000 years ago, humans began keeping the wild ancestors of the few domesticated species we are familiar with today (Zeder et al., 2006; Driscoll et al., 2009). Animal collections existed at least 4,000 years ago, with records of ancient Egyptians (Lauer, 1976), Romans (Jennison, 1937), and Greeks (Hosey et al., 2013d) keeping captive wild animals for a variety of purposes. Today, captive wild animals are still popular as pets (~42 million exotic pets are kept in the UK: Warwick et al., 2012), in zoos (Species360, 2019), and are used in research laboratories around the world (reviewed by: Mason et al., 2013).

Species differ in the way their representatives typically respond to captivity (see Table 1.1 for examples, and reviewed by: Mason, 2010). Animals from some species typically adjust well to captivity, display few behavioural problems, are long-lived, breed readily, and are easy to care for (e.g. Kenward, 1974; Couquiaud, 2005; Tarou et al., 2005; van Zeeland et al., 2009; Müller et al., 2010a). Those from other species, however, are typified by prevalent welfare-relevant management problems, e.g. behavioural and/or health issues, reduced lifespan, and suppressed reproduction, meaning they are much harder to practically care for (e.g. Kenward, 1974; Couquiaud, 2005; Tarou et al., 2005; van Zeeland et al., 2009; Müller et al., 2010a). Systematic between-species variation in captive response like this yields a benefit, in that it facilitates research. Thus, it allows testing of hypotheses relating to species-typical ecology and biology, to better understand the evolutionary drivers of the responses species typically make to captivity. Conservation biologists use such an approach to examine why species differ in extinction risk, vulnerability to human exploitation, invasiveness, and other conservation-related attributes (Fisher and Owens, 2004; Cardillo et al., 2005). Adopting a similar approach for captive wild animals can reveal what it is

intrinsically about species that results in their captive response, i.e. their typical health and/or welfare, and can inform how problems might be best addressed to ultimately improve wellbeing (reviewed in Chapter 2; for relevant examples see: Clubb and Mason, 2003; Clubb and Mason, 2007; Müller et al., 2011; Pomerantz et al., 2013; McDonald Kinkaid, 2015; Kroshko et al., 2016; Miller et al., 2018). As reviewed in Chapter 2, this approach also complements the more usual experimental and epidemiological approaches to addressing welfare-relevant research questions (also see Chapters 5 and 6 for demonstration of this).

When testing ecologically-relevant hypotheses about the captive responses of captive wild animals, it is assumed that natural selection (Darwin, 1860) has resulted in some species' attributes being genetically 'hard-wired', and evolutionary honed to maximise fitness (i.e. survival and reproductive output) (cf. Kiley-Worthington, 1989). For such attributes, *mismatches* between a species' evolutionary history and the captive environment (cf. Koene, 2013; Mason et al., 2013) might generate problems if the expression of highly motivated behaviour is thwarted in captivity (e.g. Broom, 1991); or if a species' dietary, sensory or homeostatic needs are difficult to facilitate (Morgan and Tromborg, 2007; Hosey et al., 2013c; Hosey et al., 2013f).

Table 1.1 Examples of species within taxonomic groups with differing captive responses (adapted from: Mason, 2010; McDonald Kinkaid, 2015).

Taxon	Species whose representatives typically respond well to captivity, with rationale	Species whose representatives typically respond poorly to captivity, with rationale	References
Psittacines	Some lorikeets, *Lorius* spp., and budgerigars, *Melopsittacus undulates*: Feather-damaging behaviour is uncommon Breed readily in captivity	Cockatoos, *Cacatua* or *Calyptorhynchus* spp., African grey parrots, *Psittacus erithacus*: Feather-damaging behaviour is common Breed poorly in captivity	(Schubot et al., 1992; Seibert, 2006; Garner et al., 2008; van Zeeland et al., 2009)
Raptors	Kestrel, *Falco tinnunculus*: Mortality rates "substantially lower" than in the wild; also lower than for captive sparrowhawks	Sparrowhawk, *Accipiter nisus*: Mortality rates as high as in the wild; "[susceptible] to seizures... difficult to keep"	(Kenward, 1974)
Primates	New World primate taxa, e.g. *Leontopithecus* spp., apes, e.g. *Nomascus gabriellae*, and Prosimians, e.g. *Eulemur collaris*: Reportedly present less often with Type II diabetes	Old World monkey taxa, e.g. *Cercocebus* spp.: Reportedly present more frequently with Type II diabetes	(Kuhar et al., 2013)
Pinnipeds	Grey seal, *Halicheorus gypus*: Similar survivorship in captivity as in the wild Census data suggest few breeding problems in zoos	Walrus, *Odobenus rosmarus*: Shorter lifespan than in the wild Reports and census data suggest poor reproduction in zoos	(Cornell and Asper, 1978; Dittrich, 1987; Roberts and DeMaster, 2001; Kastelein et al., 2003)
Cetaceans	Finless porpoise, *Neophocaena phocaenoides*: "Playful in captivity... successfully kept and bred"	Dall's porpoise, *Phocoenoides dalli*: "Unsuccessful in captivity, throwing itself against walls and bottom; refuses to feed,	(Couquiaud, 2005)

Taxon	Species whose representatives typically respond well to captivity, with rationale	Species whose representatives typically respond poorly to captivity, with rationale	References
		nervous, irritable, subject to infection and skin slough... probably unsuitable for captivity"	

Specific to my focus here, is whether some aspects of species' biology (i.e. their nature or genes, sensu: Johnston and Edwards, 2002) influence a species' typical response in captivity. Migratory birds provide a relevant example here. Even though migration is not required or even possible by captive individuals, birds may still attempt to migrate at the time at which their wild counterparts would. Typically, captive migrants show migratory restlessness, or 'zugunruhe', in which they repeatedly flutter and perch-hop oriented in their species-typical migratory direction and time of day (i.e. either by day or night), typically for the same time duration that the wild migratory trip would occur (Gwinner and Czeschlik, 1978; Styrsky et al., 2004; Newton, 2007). In fact, the zugunruhe intensity of captive animals is often used as a proxy for their species-typical migratory motivational strength (e.g. Eikenaar et al., 2014). So, even though captive individuals never experience migration, the influence of their migratory *nature* is such that migratory tendencies are nevertheless expressed in captivity (and, arguably, are a logical potential source of welfare problems, cf. Mason, 2010). Species' attributes associated with successful domestication provide another relevant example. A suite of specific attributes predisposed a minority of ancestral large mammal species to be suitable for domestication, resulting in the few examples of farmed domesticated species we see today (Diamond, 2017). Thus, species candidates for domestication must not be carnivorous, aggressive or easily panicked; and must be fast-growing, easily and readily bred in captivity, herd-living, non-territorial, with a well-defined linear dominance hierarchy (Clutton-Brock, 1992; Diamond, 2017). Indeed, lacking just one of these attributes renders domestication very unlikely, helping to explain failed attempts to domesticate vicuña, *Vicugna vicugna*, African buffalo, *Syncerus caffer*, and zebra, *Equus quagga*, despite most of these having domesticated close relatives (Diamond, 2017). As illustrated by these

examples, typical captive response *can* be affected by species-typical biology, and examining relationships between these might yield valuable insight into the evolutionary bases of welfare-relevant management problems.

In the upcoming sections I start by describing captive animal management problems and why they are relevant, then place them in the context of animal welfare – a topic that I also briefly review and define. After, I discuss species differences in three taxonomic groups in welfare-relevant captive management problems relating to my research question: whether species-typical foraging niche affects captive animal health and welfare. Finally, I detail the purpose and aims of my thesis.

1.2 Welfare-relevant management problems and animal welfare

Captive wild animal welfare-relevant management problems include those described in Table 1.1 and the second paragraph of this chapter. Abnormal behaviour, reduced lifespan, suppressed reproduction, and prevalent disease are all relevant examples, and are concerning from both an animal and a human perspective. Starting with the former, these types of problem are concerning from an animal perspective because of their close association with animal welfare (Broom, 1991; Dawkins, 2006; Walker et al., 2012; Mendl et al., 2017). Thus, as will be discussed in Section 1.2.1, many of these problems are indicators of individuals having suffered poor welfare. Disease-states that animals are unaware of and do not cause pain do not directly compromise welfare in themselves, e.g. pain-free cancers and obesity (Mason and Mendl, 1993; Fraser et al., 1997; and see Section 1.2.1). However, they do have potential to later become welfare problems in their own right in, e.g. if the cancer later became painful or caused other feelings of malaise; and if painful health conditions co-morbid with obesity develop, e.g. arthritis (e.g. Kuyinu et al., 2016).

From a human perspective, welfare-relevant management problems are concerning for various reasons. Captive wild animals that do not live long or breed well, whether because of poor welfare (e.g. Mason et al., 1995; Bronson et al., 2007; Peng et al., 2007; Díez-León et al., 2013) or disease (e.g. obesity: Hatt and Clauss, 2006; Schwitzer and Kaumanns, 2009), hinders attempts to maintain self-sufficient captive populations: a main aim of zoos and conservation breeding centres (Hosey et al., 2013e). Abnormal behaviours such as stereotypic behaviours (see Section 1.2.1 for definition) and self-mutilation reduce the educational value of affected zoo animals (Ormrod, 1987), can lead to pets being relinquished to re-homing centres, and are disliked by zoo visitors (Miller, 2012) and pet owners alike (Meehan, 2003; Gaskins and Bergman, 2011). Additionally, there are moral and legal obligations to ensure animals under human care are well cared for (Hill and Broom, 2009; EAZA, 2013; GOV.UK, 2013; AZA, 2018; RSPCA, 2018; WAZA, 2018).

Being fundamental to concerns over welfare-relevant management problems, next I discuss the topic of animal welfare. I begin by outlining three conceptual themes of animal welfare and define welfare in the context of this thesis. Then, being the method of measuring welfare relevant to my thesis, I discuss welfare indicators. Afterwards I provide detail on how a specific behavioural welfare indicator focussed on in this thesis – stereotypic behaviour – may arise under situations in which highly motivated behaviours are thwarted (cf. Broom, 1991), i.e. creating a mismatch (see Section 1.1 and cf. Koene, 2013; Mason et al., 2013; Mellor et al., 2018a). Finally, I describe the two welfare-relevant management problems that are the focus of my thesis.

1.2.1 What is animal welfare?

There are three main conceptual themes when defining welfare, based upon: i) naturalness of an animal's behaviour, ii) an animal's biological function and, iii) an animal's feelings (Fraser et al., 1997; Mendl et al., 2017). These themes have a degree of overlap, albeit with different fundamental priorities. To illustrate, prevention of highly motivated behaviours can lead to frustration and signs of poor welfare (Broom, 1991) such as stereotypic

behaviours (SBs) (e.g. in mice, *Mus musculus*: Würbel et al., 1996): abnormal repetitive behaviours associated with a previous or ongoing state of poor welfare (Mason, 2006b). Under the *naturalness* stance, the concern is that such behaviours are abnormal and unnatural, as they are missing from the behavioural repertoire of wild representatives (Kiley-Worthington, 1989). On *biological functioning* grounds, abnormal behaviours represent difficulty in "coping" with the captive setting (sensu Broom, 1991); may reduce productivity e.g. reproductive behaviour (stereotypic male American mink, *Neovison vison*, win fewer matings than non-stereotypic males: Díez-León et al., 2013); can exacerbate health problems (self-directed feather-plucking by captive parrots can lead to infection, blood loss, and/or hypothermia: Meehan et al., 2003b; van Zeeland et al., 2009); and may represent compromised brain function (Mason, 2006b). On a *feelings* perspective, that SBs are triggered in situations associated with suffering, such as can be presumed by frustration in this example, is the issue (Mendl et al., 2017).

Concerns over the wellbeing of animals kept in highly restricted settings, e.g. intensively farmed animals (cf. Brambell, 1965), led to the argument that welfare hinges on naturalness (Kiley-Worthington, 1989). Criticisms of this stance include that some natural behaviours only occur in negative situations, therefore detaching naturalness from welfare (Mendl et al., 2017), e.g. escaping a predator. Further to naturalness, Rollin (1993) considered that each species has a genetically encoded nature, or 'telos', and that part of what good welfare represents is animals living in accordance with their telos. This refinement was considered more welfare-relevant, if interpreted as that animals should be able to use their evolved adaptive responses when needed, developed in a species-appropriate way as per evolutionary history, domestication (if applicable) and own experiences (Fraser et al., 1997). However, an animal's evolved behavioural responses might be inadequate to cope with the challenges that captivity presents, so naturalness *per se* has limited value when assessing welfare (Mendl et al., 2017).

Considered from a biological function viewpoint, poor welfare occurs when an animal's physiological systems are disrupted to the extent that there are fitness consequences, i.e.

survival or reproduction are impaired (McGlone, 1993). Along the same lines, Broom (1986) defined welfare as the state of animal with regards to its "attempts to cope with its environment". "Coping" refers to behavioural and physiological adjustments that an animal makes based on its motivational state which, in turn, is affected by its 'needs' (Broom, 1991). Here, a need is considered a deficiency within an animal, resolvable by acquiring a resource or by responding to internal or external stimuli (Fraser and Broom, 1990). Animals might easily cope with little effort and so welfare can be considered adequate, but if coping is difficult, energetically expensive, or impossible then welfare is poor (Broom, 1986). Parameters typically used when assessing welfare from a biological function viewpoint are usefully objective and readily collected, e.g. health status, lifespan, and reproductive output (Mendl et al., 2017). However, there are three main problems associated with adopting a biological function-only stance to welfare assessment. The first is determining the point at which changes in biological function equate to difficulty or a failure to cope, i.e. poor welfare (Mendl et al., 2017). The second problem is that despite living in conditions many would consider inadequate for welfare, e.g. highly restrictive and/or unstimulating conditions, some animals function within their biological norm, meaning that these parameters can show low sensitivity in detecting poor welfare (Mendl et al., 2017). Thirdly, considering welfare purely from a biological function or fitness approach, ignores the contribution *feelings* make to an animal's state. Some have therefore proposed that physical health *and* mental wellbeing together are important to welfare (Broom, 1991; Dawkins, 2006), because feelings can be affected by poor health and *vice versa*. For example, ill feelings are associated with painful conditions such as arthritis and other chronic diseases (e.g. in humans and rats, *Rattus norvegicus*: Prugh et al., 1953; George et al., 2018).

Others argue that an animal's welfare is primarily to do with its subjective affective state or, in other words, its feelings (Duncan, 2006), and it is this definition and philosophy of animal welfare that I use in this thesis. Animals' affective states, or emotions, can be operationally defined as states "elicited by rewards and punishers, where a reward is anything for which an animal will work, and a punisher is anything that it will work to escape or avoid" (Rolls, 2013; Mendl and Paul, 2020). Key to this is that affective states are valanced, i.e. they are positive or negative (Mendl and Paul, 2020). For some, feelings take priority when assessing

welfare, over those relating to health and fitness (Duncan, 1993; Mendl et al., 2017). The underlying rationale is that if welfare is *not* about feelings, then the logic would follow that one would have to extend the same concern to plants in poor health or inadequate living conditions as is afforded to animals (Mendl et al., 2017). Most people would agree that unlike animals plants cannot suffer so we are not concerned about their welfare: it is this potential for suffering – i.e. a *feeling* – that thus is pivotal in defining welfare (Dawkins, 1990; Mendl et al., 2017). In contrast to the example from the paragraph immediately above, under this concept of welfare detrimental changes in an animal's state that do not alter the way it feels, e.g. pain-free disease, are not considered immediate welfare concerns (Mason and Mendl, 1993; Fraser et al., 1997). The feelings and biological function stances have commonalities though, in that they ultimately share many of the same concerns albeit for different reasons, e.g. most diseases and/or shortened lifespan are welfare concerns under both, but for reasons of negative affective states associated with them *versus* a decrease in effective functioning (see Table 35.1 in Mendl et al., 2017 for further examples). Directly measuring affective states in non-human animals is not possible, however, as they cannot describe what they are feeling. Instead, affective state is usually objectively assessed using validated behavioural and/or physiological indices that are sensitive to affective state (Mason, 2010), and by analogy with human brain function and behaviour (Mason and Mendl, 1993; Mendl et al., 2017).

1.2.2 Measuring welfare

Next, I discuss how welfare can be measured and because they are in line with this thesis, I restrict this discussion to welfare indicators (defined below). I do, however, acknowledge that the motivation and preference method of measuring welfare – determining what animals want and do not want – is another valuable set of tools for doing so (Dawkins, 1990; Mendl, 2001; Mendl et al., 2017), although not directly relevant here. Welfare indicators are behavioural, physiological, physical, and/or life-history parameters that are used to infer wellbeing, as they are assumed to yield information about the animal's affective state (under the biological functioning definition of welfare, they would reflect efficacy of function) (Mendl et al., 2017). A relevant example to this thesis is SB: abnormal repetitive

behaviours associated with a past or present poor welfare state (Mason, 2006b). SBs are linked with negative affective states because of the conditions in which they are initially triggered, e.g. impoverished environments (Hediger, 1950; Morris, 1964; Carlstead, 1998); being unable to perform highly motivated behaviours (e.g. in mice, *Mus musculus*: Würbel et al., 1996); to cope with and aversive or painful conditions (e.g. crib-biting horses may do so to relieve the pain of gastric ulcers: Bergeron et al., 2006); and uncontrollable stressful situations (Ödberg, 1987; Cabib, 2006). Other objective behavioural measures of affect include cognitive bias, i.e. how animals interpret and respond to ambiguous stimuli, known to be affected by emotional state in humans, with evidence for the same in animals (Harding et al., 2004; Mendl et al., 2009); and behaviours indicative of pain and disease and, so, negative affect (Mendl et al., 2017). Life-history parameters include lifespan (Broom and Johnson, 1993; Walker et al., 2012; Hosey et al., 2013b) and reproduction (e.g. Moberg, 1985) – both of which are indirectly relevant to this thesis, in Chapters 5 and 6 – because when these are reduced by disease, injury and/or chronically stressful situations, are associated with negative affective states (Mendl et al., 2017). Physiological stress responses, e.g. corticosteroid release, heart rate and blood pressure, and immune function, e.g. antibody response when challenged, are examples of physiological indices of affective state (Mason, 2010), as an elevated stress response and altered immune function are associated with negative affect (Mendl et al., 2017). Individuals vary in the way in which they respond to poor welfare conditions, e.g. SBs are prone to false negatives (or low sensitivity), as some animals become inactive instead (Fureix and Meagher, 2015; Fureix et al., 2016). Therefore, it is recommended that, ideally, a range of welfare indicators should be taken (Broom, 1986). In practice, however, time, money and practical constraints mean that most studies only focus on a select few (Mendl et al., 2017).

1.2.3 Thwarting of motivated behaviour and stereotypic behaviours

Because one of the welfare-relevant management problems focussed on in this thesis is SB next I outline how thwarting highly motivated behaviours (i.e. a mismatch; Section 1.1), such as those related to my research question, might result in SB. A given motivated behaviour sequence, such as foraging, can usually be split into two main phases: appetitive

and consummatory (Berridge, 2004). Appetitive behaviours relate to searching, e.g. a parrot flying in search of food, tend to be more variable, and indicate motivation for a particular goal (Berridge, 2004; Ball and Balthazart, 2008). Consummatory behaviours, e.g. a parrot swallowing a nut, follows appetitive behaviour, are more stereotyped in form, and represent achievement of the goal, fulfilment of motivation, and normally result in termination of the behavioural sequence (Berridge, 2004; Ball and Balthazart, 2008). Negative feedback loops control some of these behavioural sequences, e.g. if consummation is successful this leads to changes in internal state and/or cessation of response to environmental cues, and thus a reduction in motivation (Clubb et al., 2006). SBs are often thought to result from repeated failure of these negative feedback loops, leaving the animal in a state of high, unfulfilled, motivation (Clubb et al., 2006; Mason, 2006b). Stereotypic corner digging by gerbils, *Meriones unguiculatus*, is a good example of this. Wiedenmayer (1997) demonstrated that motivation for the end goal of digging, a suitable shelter, drives stereotypic digging. Gerbils provided with a sand substrate could dig but could not construct a stable burrow, and rapidly developed stereotypic digging; whereas gerbils housed without digging substrate but with a burrow, developed no stereotypic digging (Wiedenmayer, 1997). Here, without the negative feedback associated with consummation (appropriate shelter), motivation to seek shelter (by digging) persisted (Wiedenmayer, 1997). Appetitive behaviours can thus persist with the animal 'stuck' in this particular phase, and the form of the stereotypy can represent an exaggerated version of the appetitive behaviour pattern being prevented from reaching consummation (Mason, 2006b). Alternatively, consummatory behaviours might happen, e.g. feeding, even though the associated appetitive behaviours cannot be performed, e.g. searching for and/or manipulating food. If the performance of appetitive behaviours *per se* serves to reduce motivation, or if performance of consummatory behaviour has a positive feedback effect, then likewise the animal may remain in a high, thwarted motivation state (Clubb et al., 2006).

1.2.4 Welfare-relevant management problems examined in this thesis

My thesis focusses on two welfare-relevant animal management problems: SB and excessive body weight. For two chapters (3 and 4) I focus on specific forms of SB because there is evidence that they might be linked to foraging niche, and because two datasets are readily available to test hypotheses relevant to my research question (Sections 1.3.1 and 1.3.2). Also relevant to my research question is a different type of management problem: excessive body weight. Excessive body weight *per* se is unlikely to cause negative affect, and so is not a welfare concern in itself (but see: Broom, 1991 for a biological fuctioning view on this). However, when animals are overweight or, more worryingly, obese, they carry fat-levels that may impair health (WHO, 2019), leading to management problems like reduced lifespan and suppressed reproduction (e.g. Hatt and Clauss, 2006; Schwitzer and Kaumanns, 2009). Serious health problems comorbid with being overweight or obese also include those that are likely painful (e.g. Kuyinu et al., 2016): joint problems, orthopaedic disorders, and cancers (Kopelman, 2000; Hatt and Clauss, 2006; Bauer et al., 2011; Laflamme, 2012; Vaughan and Mattison, 2016; RSPCA, 2019). Therefore, it is fair to assume that for animals whose body masses are so excessive it leads to these conditions, their welfare will be compromised when they experience, i.e. feel, them.

1.3 Species differences in welfare that appear to relate to foraging niche

Foraging niche, i.e. the unique way a species uses its habitat and resources in relation to gaining food (sensu Begon et al., 2006; Slagsvold and Wiebe, 2007), and related feeding behaviours are essential to survival (Kramer, 2001). While captive animals can be considered generally well-provisioned, being regularly fed with presumably minimal starvation risk, the captive foraging and feeding environment can be very different from the one that the species evolved in several ways. The reason why such differences, or mismatches (see Section 1.1; cf. Koene, 2013; Mason et al., 2013), might be important is because of their potential to affect health and welfare.

The first potential source of mismatch relates to foraging behaviour, as some of these behaviours are unnecessary in captivity, e.g. food search and hunting, or reduced, e.g. food item handling times (Hosey, 2005). As already discussed in Section 1.2.1, thwarting or restricting highly motivated behaviours can compromise wellbeing (Broom, 1991), leading to signs of poor welfare such as SB (Clubb et al., 2006; Mason, 2006b). Relevant examples here include foraging by ungulates and other patch-feeders like parrots, who naturally spend large amounts of time foraging and whose captive foraging time budgets are typically considerably reduced in comparison (Bergeron et al., 2006). The predominant SBs in these animals are usually oral, may physically resemble the species-typical foraging mode, and often demonstrate a post-feeding peak hypothesised to represent further frustrated foraging attempts (Bergeron et al., 2006).

Nutritional differences between captive diets and those wild animals – or their ancestral equivalent – are adapted to can result in a second type of mismatch. Comparatively high sugar and calorie levels of domestic fruit compared with wild fruit, are suggested to contribute to the excessive body masses, and potential obesity, of some lemur species in captivity (Goodchild and Schwitzer, 2008). In laying hens, nutritional deficiencies contribute to abnormal feather-pecking, e.g. inadequate dietary fibre provision can affect gut motility, reduce satiety, and lead to feather pecking (Hetland et al., 2004; van Krimpen et al., 2005; Kjaer and Bessei, 2013; Rodenburg et al., 2013). In ungulates, gastrointestinal dysfunction can be caused by low-fibre high-concentrate diets, e.g. ruminal acidosis in cattle, and gastric ulcers in pigs and horses (reviewed by Bergeron et al., 2006). Such diets are also associated with oral SBs suggested, as mentioned in the paragraph immediately above, to represent unfulfilled motivation to forage – as these diets are typically quick to find and consume – but whose performance is also proposed to help alleviate symptoms of gastric discomfort (reviewed by: Bergeron et al., 2006).

Finally, enrichment studies provide indirect support for links between foraging behaviour and welfare. Foraging enrichments designed to increase captive foraging times towards those of wild animals and/or reduce amount of time spent performing SB, are well-used by

captive animals and do seem to enhance welfare (e.g. Keiper, 1969; Markowitz and LaForse, 1987; Shepherdson et al., 1989; Forthman et al., 1992; Shepherdson et al., 1993; Meehan et al., 2003b; Meehan et al., 2004; Lumeij and Hommers, 2008; Rozek et al., 2010; Rozek and Millam, 2011; van Zeeland et al., 2013). There are also examples of animals contrafreeloading: choosing to work to access food, e.g. by using searching or using manipulatory behaviours to extract food, whilst freely-available identical food is also present, e.g. maned wolves, *Chrysocyon brachyurus* (Vasconcellos et al., 2012), pigs, *Sus scrofa* (de Jonge et al., 2008), European starlings, *Sturnus vulgaris* (Bean et al., 1999) and parrots (Coulton et al., 1997).

As just reviewed, foraging niche-related mismatches have potential to affect welfare in some captive wild animals. My thesis, therefore, concerns predictors of welfare-relevant management problems in three taxonomic groups commonly held in captivity. Across these three there are examples of species differences in typical captive response, which might relate to species-typical foraging niche. For two groups (Carnivora and Psittaciformes), certain aspects of species-typical foraging niche likely result in welfare-relevant mismatches, which could explain the between-species differences observed. Furthermore, for both cases, previous comparative studies have identified aspects of foraging niche as being biological risk factors for specific signs of poor welfare. For the third group (Lemuriformes), the nature of the health problem itself and the ecology of this taxonomic group implies a possible foraging niche-related explanation. However, there are two further aspects of species-typical biology that might explain this health outcome, which I also discuss. I introduce these three taxonomic groups and their specific welfare-relevant management problems next.

1.3.1 Carnivora

Time typically devoted to route-tracing, i.e. repetitively following a set path or route within the enclosure, differs between species of captive Carnivora ('carnivores' from herein) (Clubb and Mason, 2003; Clubb and Mason, 2007; Kroshko et al., 2016). Captivity imposes restrictions on hunting which is proposed to lead to route-tracing, and there is some

evidence to support this. Firstly, route-tracing is more prevalent in carnivores than other mammalian orders (Mason et al., 2007), and this taxon also contains relatively more carnivorous species, i.e. reliant on the flesh of other animals (van Valkenburgh, 1988). Route-tracing also has a temporal relationship with captive feeding times, being usually most intensive immediately prior to feeding and ceasing afterwards (Mason, 1993; Weller and Bennett, 2001; Vickery and Mason, 2004). Additionally, hunting style might relate to route-tracing: long wild chase distances emerged as a biological risk factor for time spent route-tracing in captivity (Kroshko et al., 2016), although so did having a large home range (Clubb and Mason, 2003; Clubb and Mason, 2007; Kroshko et al., 2016; with a similar trend in: Miller et al., 2018); and enrichments encouraging chase often successfully reduce time spent route-tracing (e.g. Markowitz and LaForse, 1987; Forthman et al., 1992; Shepherdson et al., 1993). Finally, there is a body size effect: large-bodied carnivores spend relatively more time route-tracing than do small-bodied ones (Clubb and Mason, 2003; Clubb and Mason, 2007; Kroshko et al., 2016). The relevance here is that body size also relates to prey selection: at ~20kgs body mass, carnivores switch from hunting prey much smaller than themselves to hunting prey of a similar body mass to themselves (Carbone et al., 1999; Carbone et al., 2007). For species reliant on hunting for food, doing so is crucial for survival in the wild. Therefore, the potential mismatch between motivation to hunt and ability to fulfil that motivation in captivity, might explain some of the variation in species differences in route-tracing. I examine relationships between species-typical hunting and route-tracing in carnivores in **Chapter 3**.

1.3.2 Psittaciformes

Feather-damaging behaviour (FDB) prevalence varies amongst species of captive Psittaciformes ('parrots'). FDB is a typically self-directed abnormal behaviour, in which the bird chews and/or plucks its feathers (Meehan et al., 2003b; van Zeeland et al., 2009). African greys, *Psittacus erithacus,* and some cockatoo species are notably more susceptible to FDB than others, e.g. Senegal parrots, *Poicephalus senegalus* (van Zeeland et al., 2009; McDonald Kinkaid et al., 2013; McDonald Kinkaid, 2015). Bearing some demographic, environmental and morphological similarities to FDB (reviewed by van Zeeland et al., 2009;

Mellor et al., 2018a), severe feather-pecking performed by some chickens, *Gallus gallus domesticus*, in which birds painfully pull or remove conspecific's feathers (Savory, 1995; Rodenburg et al., 2013), is morphologically similar to foraging pecks (Dixon et al., 2008). Furthermore, mismatches between wild foraging activity budgets (40-75% of active time: Magrath and Lill, 1983; Westcott and Cockburn, 1988; Renton, 2001) and captive ones (captive orange-winged Amazon parrots, *Amazona amazonica*, spent ~6% of their active time eating food: Rozek et al., 2010) has also been proposed to underlie FDB (Meehan et al., 2003b; van Zeeland et al., 2009), and is widely hypothesised to result in abnormal oral behaviours across birds (Keiper, 1969; Meehan et al., 2004). A comparative study by McDonald Kinkaid (2015) confirmed that parrot species with naturally long 'relative food search times' do have more prevalent FDB in captivity, whilst relatively large brain sizes predicted prevalence of other SBs. 'Relative food search times' is a broad categorical predictor ('long' *versus* 'short') based on characteristics of the predominant food type in the species-typical wild diet (its accessibility and discoverability) (McDonald Kinkaid, 2015). This measure, however, pools two distinct aspects of appetitive foraging behaviour, i.e. food-search and -handling, which involve different mechanisms (sensu Rowland and Mathes, 2008). Therefore, understanding of the relationship between foraging niche and FDB, and how FDB might be practically best addressed is currently limited (see Chapter 2 for discussion on this topic).

Regarding wild parrot food-search and -handling behaviours, the weight of current evidence implies that restricting food-handling is the more biologically relevant regarding FDB. Structural differences between wild and captive diets provide a likely welfare-relevant mismatch. Pelleted diets are usually recommended for captive psittacines (Ullrey et al., 1991; Koutsos et al., 2001), which require little manipulation and are quick to consume (Oviatt and Millam, 1997; Meehan et al., 2003b). In the wild, parrots usually remove seed husks before eating the kernel (Ullrey et al., 1991; Koutsos et al., 2001) and accessing some items requires extensive oral manipulation (e.g. digging: Cameron, 2012) and/or crushing power and dexterity, to which some species are physically adapted (i.e. they have a suborbital arch and its associated muscle, *musculus pseudomasseter*: Homberger, 2006; Toft, 2015). Therefore, if some species are motivated to perform extensive oral

manipulatory behaviours, i.e. food handling, which are typically not supported by the captive diet, then this might manifest as FDB (sensu Clubb et al., 2006). Additionally, considering food-search and -handling as distinct aspects of foraging also permits re-examination of potential relationships between wild foraging and other forms of SB. As mentioned above, other oral SBs are also hypothesised to be linked with restriction of foraging behaviour across birds including parrots (Keiper, 1969; Meehan et al., 2004). Food search is physically limited by captivity's spatial restrictions, and is also a major driver of a species' ranging behaviour (e.g. Clutton-Brock and Harvey, 1977b; McLoughlin and Ferguson, 2000; Rolando, 2002): a biological risk factor for route-tracing in carnivores (Clubb and Mason, 2003; Clubb and Mason, 2007; Kroshko et al., 2016; with a similar trend in: Miller et al., 2018) and Primates (Pomerantz et al., 2013). Further exploring relationships between foraging and other oral SBs and route-tracing by parrots, despite McDonald Kinkaid (2015) finding these behaviours to be predicted by a different risk factor – relatively large brain volumes – is therefore worthwhile. In **Chapter 4** I investigate relationships between these two distinct phases of appetitive foraging and prevalence of FDB and other SBs across parrots.

1.3.3 Lemuriformes

Within Lemuriformes ('lemurs') species vary in susceptibility to weight gain in captivity. For example, excessive body masses are common in ring-tailed lemurs, *Lemur catta*, and blue-eyed black lemurs, *Eulemur flavifrons*, yet a healthy body condition is typical of others, e.g. greater bamboo, *Prolemur simus*, and red-bellied lemurs, *E. rubriventer* (Terranova and Coffman, 1997; Taylor et al., 2012). Excessive body weight is a welfare-relevant management problem for reasons already discussed (see Section 1.2). As positive energy imbalance, i.e. calorific intake greater than expenditure, is central to weight gain (Trayhurn, 1984; Selassie and Sinha, 2011), it seems logical that the observed species differences might relate to foraging niche (although, as will be discussed, there are other possibilities too).

Sugar and energy contents of commercial fruit are higher than those of wild fruit, proposed to contribute to the high body masses observed in some captive lemurs (Schwitzer and Kaumanns, 2001; Goodchild and Schwitzer, 2008; Junge et al., 2009). The reason why this food quality mismatch could affect some species more than others, is because of potential between-species differences in "thriftiness", or storing fat during times of plenty (i.e. "thrifty genotypes" sensu: Neel, 1962). Primates, the order lemurs belong to, like many other animals have evolved thrifty physiological adaptations to buffer against resource-restriction (Shively et al., 2009). Lemurs are native to Madagascar, where the environment is variably both harsh, e.g. soil quality and plant productivity are poor, and unpredictable, being affected by irregular events like droughts, cyclones and El Niño events (Wright, 1999). Thus, food resource availability can be both poor and unpredictable and, because this varies over the island and species' geographic ranges, could result in some species being adapted to a relatively poorer and/or more unpredictable environment than others (i.e. they are relatively thriftier). If so, these adaptations might render the same species prone to weight gain in the presumably well-provisioned captive environment. Aside from species-typical foraging niche, though, there are two alternative explanations for the observed species differences in susceptibility to captive weight gain, namely arboreality (cf. Dittus, 2013; Heldstab et al., 2016) and wild predation risk (cf. Houston et al., 1993; Witter and Cuthill, 1993; Witter et al., 1994; Kullberg et al., 1996; Higginson et al., 2012; Zamora-Camacho et al., 2014; Speakman, 2018). In **Chapter 5**, therefore, I examine whether these aspects of species-typical ecology explain species differences in susceptibility to large body masses in captive lemurs.

1.4 Purpose and aims of this thesis

The general purpose of this thesis is to examine whether foraging niche has a predictive effect on welfare-relevant management outcomes within the three taxonomic groups mentioned above. The main aims of this thesis are as follows:

I. Use phylogenetic comparative methods to identify biological risk factors for captive welfare-relevant management problems within Carnivora, Lemuriformes, and Psittaciformes.

II. Make tailored husbandry, housing, and enrichment recommendations based on successful identification of biological risk factors, hopefully to improve the wellbeing of thousands of individuals across different species.
III. Use findings to extrapolate beyond current datasets to predict how species new to captivity may respond; and/or suggest types of species currently within collections that might be also be predisposed to the problems examined here.
IV. Use findings to assist in collection and population management decision-making, by suggesting species pre-adapted to be ill-suited to captive conditions.
V. Illustrate the strengths and weaknesses of using phylogenetic comparative methods in addressing animal welfare-relevant questions: a relatively novel research approach in this subject area.

1.4.1 Chapter outlines

To meet my general purpose and aims just described, this thesis contains the following chapters:

In **Chapter 2** I review the use of phylogenetic comparative methods in addressing animal welfare-related research questions.

In **Chapter 3** I examine the role foraging niche might have in explaining differences in species-typical route-tracing severity across 27 carnivore species. The main purpose of this chapter is to test hypotheses on the restriction of behaviours relating to hunting. Secondary to this, I also explore whether the aspects of foraging niche examined in this chapter explain any of the variation in route-tracing severity not explained by annual home range size (a biological risk factor for route-tracing: Clubb and Mason, 2003; Clubb and Mason, 2007; Kroshko et al., 2016; with a similar trend in: Miller et al., 2018).

The main purpose of **Chapter 4** is to establish whether the restriction of food-search *or* -handling foraging behaviours predicts prevalence of feather-damaging behaviour, other oral stereotypic behaviours and/or route-tracing across 50 parrot species. Secondary to this, to inform the analyses associated with the final purpose of this chapter, I explore relationships between prevalence of subtypes of other stereotypic behaviours, and between these and

feather-damaging behaviour. Afterwards, I then assess whether foraging behaviour explains any of the variance in other types of stereotypic behaviours, not explained by relative brain volumes (a previously identified biological risk factor for them: McDonald Kinkaid, 2015).

My purpose in **Chapter 5** is to understand why there are species differences in susceptibility to captive weight gain across 13 lemur species, using a proxy for body condition: 'relative body mass', i.e. the ratio of captive body mass to species-typical wild body mass (after: Taylor et al., 2012). I explore a range of potential biological risk factors for large species-typical relative body masses, by testing two foraging niche-related hypotheses and two alternative hypotheses relating to other aspects of species-typical biology.

Following from Chapter 5, in **Chapter 6** I use an epidemiological approach to examine individual-level risk factors for large relative body masses in a subset of four of the Lemuriform species whose data I used in the previous chapter.

Finally, in my overall Discussion, **Chapter 7**, I summarise my main findings and how they relate to my stated aims, describe the limitations of my studies, and detail future research.

Chapter 2: Phylogenetic comparative methods: harnessing the power of species diversity to investigate welfare issues in captive wild animals

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Sections of this chapter not primarily my own work, are clearly referenced to their sources. The division of labour between co-authors were as follows:

Emma Mellor: background literature review, wrote first draft, edited Figures for the paper, and edited text after Reviewers' comments.

Georgia Mason: edited drafts before and after Reviewer's comments, produced two Tables.

Heather McDonald Kinkaid: supplied one Figure (Fig. 2.3), another is based on her original (Fig. 2.2), and commented on the draft of this manuscript prior to submission.

Abstract

This chapter reviews a way of investigating health and welfare problems in captive wild animals (e.g. those in zoos, aviaries, aquaria or aquaculture systems) that has great potential, but to date has been little used: systematically comparing species with few or no health and welfare issues to those more prone to problems. Doing so pinpoints species-typical welfare risks and protective factors (such as aspects of their natural behavioural biology), information which can then be used to help prevent or remedy problems by suggesting new ways to improve housing and husbandry, and by identifying species intrinsically best suited to captivity. A detailed, step-by-step 'how to' guide is provided for researchers interested in using these techniques, including guidance on how to control statistically for the inherent similarities shared by related species: an important concern because simple, cross-species comparisons that do not do this may well fail to meet statistical assumptions of non-independence. The few relevant studies that have investigated captive wild animals' welfare problems using this method are described. Overall, such approaches reap value from the great number and diversity of species held in captivity (e.g. the many thousands of species held in zoos); can yield new insights from existing data and published results; render previously intractable welfare questions (such as "do birds need to fly?" or "do Carnivora need to hunt?") amenable to study; and generate evidence-based principles for integrating animal welfare into collection planning.

2.1 Introduction

Ensuring good animal health and welfare is part of the ethos of modern zoos (Hill and Broom, 2009; EAZA, 2013; AZA, 2018; WAZA, 2018) Indeed, the World Association of Zoos and Aquariums (WAZA) states: "zoos and aquariums have a responsibility to achieve high standards of animal welfare" (Mellor et al., 2015). This reflects moral and legal obligations that animals kept by humans should be well cared for (e.g. Hill and Broom, 2009; GOV.UK, 2013; RSPCA, 2018). But good welfare yields practical benefits too. For example, good animal welfare improves the public's perception of captive facilities (e.g. Miller, 2012) and also helps zoos meet their aims of achieving self-sustaining populations (Hosey et al., 2013e) by ensuring that as many individuals as required successfully mate and produce viable progeny. This is because poor welfare can compromise libido, fertility, parental care, and survivorship (e.g. Mason et al., 1995; Bronson et al., 2007; Peng et al., 2007; Díez-León et al., 2013).

Zoos keep a vast, diverse taxonomic array of animals. For terrestrial vertebrates alone, Species360 (Species360, 2019) member zoos hold nearly 4,000 species (Conde et al., 2013) and, therefore, species-specific, specialised research is often required to optimise husbandry. Zoo health and welfare researchers have three main research methods at their disposal, two of which are already commonplace. One is experimental. Here, the effects of experimentally providing a treatment are recorded, with subjects often acting as their own controls. Examples include studies of the effects of UV provision on broad-snouted caiman (*Caiman latirostris*, Daudin, 1802) (Siroski et al., 2012); of carotenoid supplementation on southern corroboree tadpoles (*Pseudophryne corroboree*, Moore, 1953) (Byrne and Silla, 2017); of dietary manipulations on lemurs (Britt et al., 2015); and myriad environmental enrichment studies (e.g. Wallace et al., 2013; Schneider et al., 2014). Similar 'pseudo-experimental' research instead opportunistically studies the effects of non-experimental manipulations, such as the impacts of visitor-generated noise (e.g. Quadros et al., 2014) and inter-zoo transfers (e.g. Schmid et al., 2001; Snyder et al., 2012).

The second common research approach is epidemiological. Here, unplanned, pre-existing variation in various aspects of husbandry or health care is used in a between-subject approach (e.g. comparing animals across different enclosures or zoos). Examples include: Blay and Côté (2001)'s survey of enclosure-related effects on breeding and mortality in Humboldt penguins (*Spheniscus humboldti*, Meyen, 1834); research into effects of birth origin on the survivorship of zoo elephants (*Loxodonta africana*, Blumenbach, 1797; Elephas maximus, Linnaeus, 1758) (Clubb et al., 2009); and recent multi-zoo studies of housing- and husbandry-related risk factors for stereotypic behaviour in polar bears (*Ursus maritimus*, Phipps, 1774) (Shepherdson et al., 2013) and elephants (Greco et al., 2016).

The third research approach is the focus of this chapter and used throughout my thesis: exploring the correlates of variation across different species (where 'species', rather than individual, enclosure, or zoo, is the unit of replication). Like epidemiological approaches, this methodology exploits pre-existing variation in health and welfare problems: here, variation between different species. It then seeks to identify what makes some species prone to welfare problems in captivity, but others – sometimes even closely related species – instead resilient and apparently protected from such issues. Conservation biologists working on in situ populations have long used this approach to reveal why species differ in extinction risk, vulnerability to human exploitation, invasiveness, and other conservation-related attributes (Fisher and Owens, 2004; Cardillo et al., 2005), and it has huge potential for advancing the understanding of zoo animal welfare (Clubb and Mason, 2004; Mason, 2010). However, this approach has been relatively little used to date, perhaps because it requires formal "phylogenetic comparative methods" (PCMs): statistical methods permitting correct statistical comparison across species (e.g. Cornwell and Nakagawa, 2017).

The purpose of this review is therefore to provide an introduction to PCMs tailored for researchers interested in studying welfare problems in zoos, aquaria, and similar systems. First, I first explain how, if used naïvely, research into between-species variation can fail to meet statistical assumptions of non-independence; why this matters; and how this problem

can be solved statistically. I then describe the few studies to investigate captive wild animals' welfare problems using PCMs. Next I provide a step-by-step 'how to' guide to using these techniques, including how to control statistically for the non-independence of related species. To end, I discuss how this approach for understanding and improving animal welfare can complement other methodologies, and how it may even have unique value, making previously intractable questions tractable and providing principles to assist collection planning.

2.2 Why use "phylogenetic" comparative methods when comparing species?

The principle behind comparing species to test welfare-related hypotheses is quite simple. If, for example, one wanted to test the hypothesis that being able to fly is important for avian welfare, one would collect data on welfare indicators (e.g. stereotypic behaviour, egg hatchability, chick mortality, or the prevalence of opportunistic infections, cf. Hill and Broom, 2009; Mason and Veasey, 2010; Appleby et al., 2018) from a range of species that differ in reliance on flight in the wild. If being able to fly is important for captive bird welfare, this makes the testable prediction that naturally flightless species should have the best captive welfare (because they have no flight behaviour to be constrained); while species that fly a lot, for example relying on flight to feed or migrate, should have the poorest welfare, because naturally strong flying motivations are frustrated. This thus predicts a positive relationship between metrics of species-typical reliance on flight in nature and species-typical captive welfare problems (see Figure 2.1A).

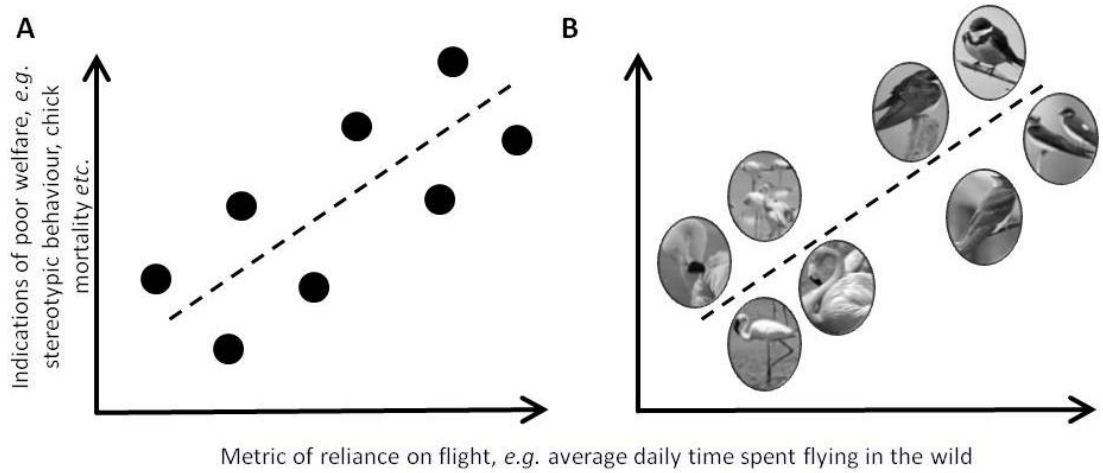

Figure 2.1. Hypothetical example of an investigation between species-typical biology and species-typical welfare. In this hypothetical example, a researcher wishes to investigate the relationship between reliance on flight (in this case measured as daily flight time) in the wild, and signs of poor captive welfare. A) At first glance, there appears to be a positive correlation between the two (though one would like a larger sample size than eight; see Section 2.4.2). This might lead the researcher to naïvely conclude that being heavily reliant on flight is a risk factor for poor welfare in birds. B) However, here it is clear that rather than eight independent datapoints, we have two clusters of closely related species, so effectively reducing our sample size to just two. Before inferring any relationship between daily flight time and welfare, one must first control for non-independence amongst the species by statistically accounting for phylogeny (see Section 2.2). Photo credits: www.pixabay.com

However, the simple regression depicted in Figure 2.1A is inappropriate. Recognised for decades (e.g. Clutton-Brock and Harvey, 1977a), comparing species as though each is an independent datapoint (a key assumption of most standard statistical tests) is problematic. This is because species are part of hierarchical structures (or 'phylogenies'), and so typically cannot be considered independent from each other (Felsenstein, 1985; Grafen, 1989; Martins and Garland, 1991; Purvis and Rambaut, 1995; Harvey and Rambaut, 1998). Such shared ancestry often results in non-independence, or pseudoreplication (Hurlbert, 1984), because closely related species are likely to resemble each other, sharing similar biological and non-biological attributes (Harvey and Pagel, 1991). This similarity based on relatedness is termed 'phylogenetic signal' (Grafen, 1989; Pagel, 1999; Blomberg et al., 2003). If this is ignored and standard statistical tests used, species are incorrectly assumed to be

statistically independent (Diaz-Uriarte and Garland, 1996; though see: Revell, 2010), and phylogeny may confound the analysis.

Why this matters is illustrated by the (fictitious) data in Figure 2.1B. This reveals that the data shown in Figure 2.1A come from two separate groups of closely related species which cluster together, effectively reducing our eight (pseudoreplicative) datapoints to just two groupings of similar birds. The flamingo species are all intrinsically similar to one another in their low reliance on flight, but also in being large-bodied, aquatic filter-feeders, dramatic-looking to human visitors, etc. Likewise, the swallows are all intrinsically similar to each other in their heavy reliance on flight, but also in being small-bodied, insectivorous, duller in appearance to humans, etc. Ignoring phylogeny thus makes it impossible to validly assess whether there is a correlation between daily time spent flying and signs of poor welfare, because any of the attributes that flamingos share with one another (and do not share with swallows) might equally explain the apparent relationship (cf. Cuthill, 2005). Our fictitious example thus reveals the regression in Figure 2.1A to be a Type I error: there is no convincing evidence that constraints on flying predict poor welfare, because within each group, the relatively greater fliers do not have the poorest welfare. Thus, after parsing out phylogenetic relatedness, different patterns can emerge from species data; and when they do, these are the ones that test hypotheses validly.

But how to parse out such relatedness statistically? Felsenstein (1985)'s seminal paper was the first to show how to statistically solve this problem by incorporating phylogenetic relationships between species into analyses. This paper presented a method called 'phylogenetic independent contrasts' (see "Data analysis and interpretation", below, for details), and thus 'phylogenetic comparative methods' (PCMs) were born. PCMs have since undergone rapid development, with various options now available, such as 'phylogenetic generalised least squares regressions' (Grafen, 1989) (see "Data analysis and interpretation", below, for details). Are PCMs essential when comparing species to test hypotheses? The simple answer is yes, to avoid pseudoreplication. PCMs have thus robustly

withstood criticism from some (e.g. Westoby et al., 1995; Björklund, 1997). Furthermore, not using PCMs to analyse species data can alter results. Simulation studies repeatedly demonstrate that PCMs out-perform standard statistical tests (e.g. Revell, 2010), reducing both Type I (e.g. Diaz-Uriarte and Garland, 1996) and Type II error rates, so increasing statistical power (Arnold et al., 2010). PCMs are therefore widely accepted as the correct way to analyse species data when testing hypotheses (with Felsenstein's seminal paper since accruing over 5,500 citations, Web of Science (WoS, 2018) accessed 03/20/18), and are mainstream research tools for evolutionary biologists and behavioural ecologists (reviewed by Freckleton, 2009; Cornwell and Nakagawa, 2017).

2.3 PCMs and welfare issues in captive wild animals: an overview of past research

PCMs have started to be used to investigate captive wild animal welfare issues, testing hypotheses about risk factors by correlating species-typical attributes (typically aspects of wild behaviour, biology or ecology: candidate predictor variables) with measures of species-typical welfare (e.g. captive animals' infant mortality rates or behavioural problems: outcome variables). I summarise these studies next.

Focusing on captive Carnivora, Clubb and Mason (2003, 2007) collated data on stereotypic behaviour across 33 species. After tests for serial independence to assess similarity between pairs of species (Abouheif, 1999), the authors used phylogenetic independent contrasts (PICs) to test two broad hypotheses. One was that wide-ranging species are at risk of stereotypic route-tracing (an idea proposed decades earlier by canid researchers [Forthman-Quick, 1984]); the other, that restricting hunting compromises well-being. Their analyses revealed that travelling large distances in the wild, and being both large-bodied and wide-ranging, were risk factors for route-tracing and elevated captive infant mortality (CIM). Reliance on hunting, in contrast, seemed not to predict poor captive welfare. The authors suggested that these results could inform collection planning: "it might be sensible – both

more cost-effective and humane – for zoos to focus on those carnivores inherently best suited to current, or at least readily achievable, enclosure sizes and enrichment/husbandry regimes. Wide-ranging species instead could be conserved in specialized breeding centres … or instead via in situ approaches" (Clubb and Mason, 2007). They also proposed that mimicking aspects of wide-ranging carnivores' lives could enhance well-being via "substantial increases in space; greater numbers of viewpoints; …more spatial and/or stimulus complexity and less day-to-day environmental predictability — combined (importantly) with the ability of the animals to control their own access to such increased variability; and more scope to approach or retreat from the public, conspecifics, and other stimuli, at will".

Capitalising on new PIC software, a larger database, and an updated phylogeny, Kroshko et al. (2016) replicated this work. They confirmed the relationship between route-tracing and large daily travel distances/home range sizes, but found the latter no longer depended on body size, and that the daily travel distance effect was a mere by-product of home range size. This suggests the relationship between home range size and route-tracing is not mediated by active locomotion, leading the authors to re-emphasize the likely value of husbandry enhancements designed to emulate the variety and control wide-ranging animals likely experience in the wild. Long chase distances also now tentatively emerged as a risk factor for route-tracing, albeit from a sample size of just five species. CIM, however, was no longer predicted by any aspect of wild biology, leaving the great variation in species-typical Carnivora CIM "an urgent topic for future work, one best addressed using both a broader range of species-typical potential risk factors and [ZIMS] data on infant mortality". Partly to look at this, species differences in Carnivora welfare are now being re-investigated, incorporating six more years of data and applying a newer PCM approach, phylogenetic generalised least squares (PGLS) regressions (Chapter 3 and Bandeli, 2018).

Next to use PCMs in the context of captive animal welfare was a Swiss team who, with collaborators, investigated patterns in the mortality rates of zoo-housed ruminants. Their

main PCM study applied PGLS to 78 Ruminantia species (Müller et al., 2011). Each species' average captive life expectancy, expressed as a proportion of its maximum recorded life expectancy ('relative life expectancy': rLE) was used to assess husbandry success (Müller et al., 2010b; Müller et al., 2011). Several hypotheses were tested about risk and protective factors for rLE, the authors arguing that results could help to optimise husbandry and identify types of species for which "a higher husbandry success can more easily be achieved". In later complementary studies, senescence rates (albeit combining non-PCM with PCM [PGLS] analyses) (Lemaître et al., 2013) and seasonal mortality patterns (Carisch et al., 2017) were also examined for many of the same species.

One important hypothesis tested was that the intensive population management related to having a studbook would enhance rLE. This was supported: studbook-managed species had significantly longer rLEs than non-studbook species (Müller et al., 2011). Turning to intrinsic aspects of biology, two plausible hypotheses were rejected. One rejected hypothesis was related to natural social structure: that "…density-dependent influences on LE (social stress, contact with pathogens) should have a higher impact in solitary and pair-living species, which are less adapted to crowded conditions (as in zoos)". Their second non-supported hypothesis was that, because most relevant zoos were located in temperate regions, tropical species would have reduced rLE. Results instead "indicat[ed] that climatic stress in (sub-)tropic species that are kept in the temperate zone does … not play an important role". Subsequently, Carisch et al. (2017) similarly found that the latitude of a Ruminant species' origin (across 88 species) did not appear to predict over-winter mortality rates in zoos.

The fourth hypothesis tested by Müller et al. (2011) was supported. Mating system affected rLE: males from polygynous species were found to have reduced rLEs. Carisch et al. (2017) similarly found some apparent effects of mating system on seasonal mortality at the onset of rut in zoo-housed cervids of both sexes, leading them to advise that "husbandry measures aimed at protecting females from rutting males are important, especially in cervids".

Finally, a fifth, dietary-related hypothesis was also supported, inspired by a previous non-PCM result from deer suggesting that grazing species have longer rLEs in zoos than browsing species (Müller et al., 2010b). In Müller et al. (2011) the same pattern emerged for female Ruminants: naturally grazing species were longer-lived in captivity, thus corroborating "the subjective experience that browsers demonstrate a higher nutrition-related mortality in captivity and are more challenging to keep when compared with grazing species, owing to the complex logistics of providing browse". Lemaître et al. (2013) subsequently analysed senescence rates in a subset of 22 species for which age-specific wild mortality data were also available. Typically, aging rates were lower in zoos than in the wild, but this difference was most marked for grazers (of both sexes). These authors concluded "this indicates that animals in zoos perform the better compared to free-ranging conditions the more they are grazers" and emphasised again "the difficulty of keeping browser species in captivity".

The final examples come from studies on primates and the sole avian welfare PCM study. Across 24 primate species, Pomerantz et al. (2013) used PGLS to reveal that, somewhat similar to the first Carnivora study (Clubb and Mason, 2003; Clubb and Mason, 2007), long wild daily travel distances tended to predict stereotypic route-tracing. Additionally, large natural group sizes predicted another abnormal behaviour, hair-pulling. These researchers argued that such research "facilitates detection of the more 'susceptible' species, as well as enabling the decision-makers to focus on specific environmental factors in order to improve the primates' psychological welfare." Specific husbandry recommendations were for activity levels to be increased (for instance via "incorporating modular structures within the enclosure, allowing for easy and frequent change of the environment"), along with the creation of "more opportunities for positive social interactions for the animals. Where possible, it is recommended to house groups in numbers similar to those reported in the wild."

Lastly, McDonald Kinkaid (2015) applied PICs to 201 Psittaciform (parrot) species kept by aviculturalists or as pets (work currently being replicated using PGLS and an updated

phylogeny: McDonald Kinkaid et al., in prep.) Unlike the primate study, she found no effect of sociality; however, naturally effortful modes of foraging and relatively large brains (a proxy for intelligence), were both risk factors for stereotypic behaviour in captive pet parrots. Furthermore, naturally effortful modes of foraging also predicted reduced captive.reproductive success, as did being classed as 'endangered', with a trend for similar effects of brain size. The author concluded: "We can use this information to make informed predictions about the suitability for captivity of different species … my findings suggest that the two best predictors of this should be high natural foraging effort and large relative brain volume, such that species characterized by either one (or both) of these risk factors are intrinsically predisposed to adjust relatively poorly to captive conditions". In terms of husbandry improvements, McDonald Kinkaid recommended supplying more naturalistic diets, and enrichment opportunities to learn and problem solve. She added, "it would now be useful to perform comparative analyses for other similarly large-brained or relatively intelligent taxa – like corvids, primates, or cetaceans – in order to determine whether some of the same biological risk factors identified for parrots also predict relatively poor welfare among those groups". This highlights some of the exciting research questions that PCMs are uniquely able to tackle (and more are suggested in Table 2.1).

2.4 Using PCMs to test welfare-relevant hypotheses: a step-by-step guide

This section provides a 'how to' guide for future welfare studies, based on the studies just described, other relevant studies using zoo data, and PCM studies from other fields.

2.4.1 Hypothesis generation

As with any research, the first step is specifying the hypotheses and their predictions, since these determine precisely which data are required (e.g. which specific species-level variables need quantifying). This might involve devising new hypotheses by reading about the species and welfare problems of interest, or instead identifying pre-existing hypotheses

from the literature. Table 2.1 lists several published, but as yet untested, research ideas and their predictions: all ideal topics for future PCM studies.

Some specific hypotheses may arise from speculating about behavioural needs (like the 'does restricting flight affect bird welfare?' example earlier; or the question, 'do carnivores need to hunt?' see Table 2.1). Others may be inspired by patterns of unexplained variation in species-typical welfare. As we saw above, for instance, it was apparent differences between species that led to the testable hypotheses that being wide-ranging is a risk factor for route-tracing, and that being a browser predicts relatively short captive lifespans (with similar species differences generating the hypothesis that prey species hide their pain; see Table 2.1). In other cases, observed variation in captive welfare may prompt more open-ended research, with an array of competing hypotheses being tested. Why captive carnivores show such variation in captive infant mortality is one case in point, potential predictors being any factor that could stress carnivore mothers, and /or make infants more or less vulnerable to premature death.

Table 2.1 Table outlining pre-existing published but as yet untested hypotheses relevant to zoo animal welfare. All of these could be addressed using PCMs (from Mellor et al., 2018b).

Hypothesis	Taxa	Prediction	Measurable predictor variable(s) for testing the prediction
Attributes related to ecological or behavioural plasticity:			
Ecological generalism preadapts species to good welfare in captivity (Mason et al., 2013)	All	Generalists should have better welfare[†] in captivity than specialists	Number of habitats found in; geographical range; latitudinal range
Resilience / adaptability to environmental change preadapts species to good welfare in captivity (Mason et al., 2013)	All	Species that can cope with sudden environmental change in the wild should have better welfare[†] in captivity than species which cannot	Whether or not species persist/thrive when exposed to urbanisation; whether or not invasive (corrected for 'propagule effects', sensu: Veltman et al., 1996); whether or not thrives after reintroduction attempts (again, corrected for 'propagule effects': Veltman et al., 1996)
Species with low cognitive complexity/ behavioural flexibility will be too inflexible to adjust to captivity (Maple, 1979)	All	Species with low cognitive complexity / behavioural flexibility should have poorer welfare[†] in captivity than more those with greater cognitive complexity/behavioural flexibility	Relative brain volume; measures of behavioural innovation rates (from e.g. Lefebvre and Sol, 2008; Lefebvre et al., 2013; Ducatez et al., 2015)

Hypothesis	**Taxa**	**Prediction**	**Measurable predictor variable(s) for testing the prediction**
Captive environment is too unstimulating ('boring') for species with greater cognitive complexity/behavioural flexibility (Maple, 1979; Grimm, 2011)	Primates (Maple, 1979) & Cetacea (Grimm, 2011)	Species with greater cognitive complexity/behavioural flexibility should have poorer welfare† in captivity than those with low cognitive complexity behavioural flexibility	As above
Attributes related to being a prey species:			
Prey species hide their pain from observers (Kahn and Line, 2007)	All	Prey species should be at higher risk of what human carers perceive as sudden instances of severe illness or death; while non-prey species have longer periods of detectable clinical illness	Whether or not prey species as adults; whether typically predated by sight /auditory cues
Fear of humans predisposes species to poor welfare in captivity (Hediger, 1950)	All	Bold species should have better welfare† in captivity than timid species	Flight distance from stressors (especially humans); whether or not species is stressed by ecotourism (Mason, 2010)
Attributes related to ranging behaviour:			
Restrictions on travelling long distances compromise welfare (Couquiaud, 2005)	Cetacea	Coastal (shallow water), little-ranging species should have better welfare† in	Daily/annual distances travelled; maximum distances travelled from coast to open-ocean; coastal *versus* pelagic

Hypothesis	**Taxa**	**Prediction**	**Measurable predictor variable(s) for testing the prediction**
		aquaria than open-ocean pelagic (deep water) species	
Restrictions on ranging and/or migration compromise welfare (Mason, 2010; Mason et al., 2013)	Psittaciformes (but potentially all birds)	Little-ranging, resident species should have better welfare in captivity[†] than widely-ranging and/or migratory ones	Daily distances travelled (including for species that do not fly); migratory *versus* resident.
Restrictions on ranging compromise Callitrichidae welfare (Mason and Mendl, 1997)	Marmosets and tamarins	Naturally wide-ranging callitrichid species should have poorer[†] welfare in laboratories and zoos than naturally little-ranging species	Daily distance travelled; typical home-range size
The home range effect on stereotypic route-tracing relates to a lack of control and/or novelty in the captive environment (Kroshko et al., 2016)	Carnivora	Relatively nomadic species should show more route-tracing in captivity than species whose annual range is very similar to their daily range	Ratio of daily ranging:annual ranging; annual number of den sites used; number of habitat types typically experienced by wild individuals (Kroshko et al., 2016)
Attributes related to natural foraging niche:			
Hunting behaviour is a behavioural 'need' that gives rise to stereotypic route-tracing (Kroshko et al., 2016)	Carnivora	Pursuit hunters should be at higher risk of route-tracing than species with other	% day spent hunting; prey chase distance; hunting style; top speed when hunting; killing methods used;

Hypothesis	**Taxa**	**Prediction**	**Measurable predictor variable(s) for testing the prediction**
		hunting style / species that do not hunt at all	gaits used during chase; eating patterns used post-kill (Kroshko et al., 2016)
Post-feeding oral stereotypic behaviours derived from localised food searching (Mason and Mendl, 1997; Mason, 2010)	Ungulata and other taxa containing patch-feeders	Species that are typically patch-feeders should be at higher risk of abnormal oral behaviours (e.g. tongue-rolling) than species that graze or browse less selectively	Patchiness of food; ratio of time spent searching: time spent consuming food
Regurgitation and reingestion relates to not being able to 'trickle-feed' as in the wild (Struck et al., 2007)	Primates	Species that spend more time feeding in the wild should be more likely to show regurgitation and reingestion than species which naturally spend little time feeding	Time spent foraging; number of eating bouts per day
Dietary generalism preadapts species to good welfare in captivity (Mason, 2015)	All	Dietary generalists should have better welfare[†] in captivity than dietary specialists	Degree of dietary specialism
Attributes related to other types of natural behaviour:			

Hypothesis	**Taxa**	**Prediction**	**Measurable predictor variable(s) for testing the prediction**
Welfare problems relate to restricted flying in captivity (Schmid et al., 2006; Mellor, 2014)	Psittaciformes (but potentially all birds)	Species highly reliant on flight should have poorer welfare† in captivity than species that naturally show little or no flight	Number of hours spent flying/day in the wild; size of flight muscles in wild birds; natural reliance on flight to feed; natural reliance on flight to migrate
Restrictions on arboreality compromise Callitrichidae welfare (Prescott and Buchanan-Smith, 2004)	Marmosets and tamarins	Species that naturally use higher regions of the forest canopy and/or little use the forest floor should have poorer† welfare in captivity than species that naturally use lower parts of the canopy and the forest floor	Canopy levels used; ratio of time spent on forest floor: in trees; nest height in the wild
Restrictions on diving compromise welfare in Cetacea (Couquiaud, 2005)	Cetacea	Shallow water species should have better† welfare in aquaria than deep water species	Maximum dive distance; number of dives per day; maximum time spent at maximum depth underwater

† Welfare could be assessed via e.g. good reproductive outputs; long lifespans; low stereotypic behaviour etc. (see Section 1.2.2).

2.4.2 Data collection when using PCMs: general considerations

A single summary statistic is usually calculated, one per species, for all variables, and including as many species as possible maximises power. Blomberg et al. (2003), for example, argue that ideally at least 20 species are required for acceptable power and Type I error rates. Examples of species-level summary statistics might include (depending on the hypotheses under test): median home range size, whether or not a prey species, and/or median enclosure size (as potential predictor variables); and typical life expectancy, reproductive output, and/or median time budget spent on stereotypic behaviour (as potential outcome variables). Where appropriate, median values are recommended over means, to reduce effects of outliers and skew in the raw data (Gittleman, 1989).

A key assumption of species-level summary statistics is that they do represent species-typical norms (Ives et al., 2007): thus assuming that either intra-specific (within species) variation is absent (Ives et al., 2007; Garamszegi, 2014), or the population has been sampled well enough that intra-specific variation is well-captured in the data (e.g. Garamszegi, 2014). However, intra-specific variability can sometimes be rather large (e.g. for behavioural traits), and biases can be introduced by, for instance, data collection differences, sub-population differences, and small and/or unequal sample sizes between species (Garamszegi and Møller, 2010). Practical ways to minimize such effects of intra-specific variation are to use data from as many individuals from as many locations as feasible; and/or to impose a minimum sample size of individuals per species (on determining suitable intra-specific sample sizes and for analyses overall see: Garamszegi, 2014). For example, in the Kroshko et al. (2016) and McDonald Kinkaid (2015) studies, for inclusion each species had to have outcome variable data for ≥5 individuals; while in Müller et al. (2010b); Müller et al. (2011) the minimum was 45. Another possible solution, though not always feasible, is to account statistically for intra-specific variation and sampling error (Symonds and Blomberg, 2014) which then improves the estimation of parameters when models are run (Ives et al., 2007) – an approach touched on further below (Section 2.4.7).

Next I describe potential sources of and methods for collecting data on health and welfare outcome variables, outlining the benefits and limitations of each. After this, I turn to potential predictor variables.

2.4.3 Outcome variable: data collection

2.4.3.1 Accessing zoo-generate dataset, e.g. ZIMS and studbooks

Captive infant mortality rate values in the Carnivora studies (Clubb and Mason, 2003; Clubb and Mason, 2007; Kroshko et al., 2016) were extracted from International Zoo Yearbooks, which published infant mortality reports. This practice stopped in 2000, however, making this data source increasingly historical. In collaboration with individual zoos, veterinary records can also be useful sources of data relating to health and disease (e.g. Miller et al., 2016). For longevity and mortality data, studbooks (in collaboration with species' studbook keepers) are also potentially useful, though not used in PCM research as yet. An alternative, up-to-date, and far more extensive source of data is the Zoological Information Management System (ZIMS), a worldwide member zoo database. Research requests can be made to "Species 360" (formerly the International Species Information System [ISIS]) for ZIMS husbandry- or veterinary-related data and studbook information on individuals from many thousands of species (Species360, 2018). ZIMS data can potentially provide impressive statistical power, and also widely samples global populations. For example, access to ZIMS data allowed Müller et al. (2011), to create a dataset of 166,901 individuals across 78 species for their Ruminantia study. However, if planning to use ZIMS data, one practical consideration is that applications for access can take up to a year to be processed, and may be denied (e.g. Kroshko, 2015; McDonald Kinkaid, 2015). For relatively short-term studies, such as PhD projects, relying on such data is therefore unwise.

Whatever the source, data must always be checked for errors. In ZIMS, for example, husbandry and veterinary data quality and type can vary between collections; birth and death records can be missing; and animals may be lost to audit when moved between

institutions (Mace and Pelletier, 2007; L. Rowden, pers. comm., 2015). Therefore, data should be checked for obvious errors and internal consistency, and ideally cross-referenced with other sources and/or validated by contacting zoos holding individuals with dubious entries (e.g. Clubb et al., 2009). Questionable data that cannot be corrected by such means should be excluded.

2.4.3.2 Surveying animal carers, e.g. keeping staff

Surveys can cheaply, efficiently gather data on many animals from many collections (Munson, 1993; Lewis et al., 2010): ideal for PCM studies. For example, using an online survey of pet owners, McDonald Kinkaid (2015) quite rapidly collected data on stereotypic behaviour and medical conditions for over 1,400 individual pet parrots from 74 species worldwide. Surveys can also capture a large sample of the overall population, making them good for assessing prevalence (% affected animals), since this measure only requires simple yes/no answers from respondents. However, time demands on animal care staff must be considered: zoo surveys, for instance, should be designed thoughtfully to not over-burden staff time and enhance chances of good return rates (see Plowman et al., 2006). Surveys are less effective for quantitative data like behavioural time-budgets, since it is unrealistic to expect participants to make lengthy behavioural observations. Noise is also likely to affect survey data, due to idiosyncratic responses and different interpretations of the focal measures from different people, although this can be mitigated by surveying numerous species and building up large sample sizes for each one.

2.4.3.3 Extracting data from published research

Using ready-published data is efficient and can also allow coverage of diverse collections worldwide. The Carnivora studies extracted observational data on stereotypic behaviour from 173 studies using this method (Clubb and Mason, 2003; Clubb and Mason, 2007; Kroshko et al., 2016) yielding data on over 1,300 individuals across 51 species from collections worldwide. For each species, values were summarised across individuals to calculate a single statistic: median % observations spent stereotyping by affected animals.

McDonald Kinkaid (2015) likewise used publications to obtain Psittaciform reproduction data: captive hatch rates for 122 species from North America and, using an expert technical report, the relative breeding difficulty of 141 species.

This approach has limitations, however. If combining multiple sources, data will not be standardised (cf. Garamszegi and Møller, 2010), necessitating quality checks. For instance, for behavioural data, included studies should use consistent data collection methods, and arguably focus on stably housed subjects (since recent changes in e.g., social grouping or enrichment, may affect how representative behavioural data are). The resulting dataset will likely contain gaps, with some species being well-represented but others under-sampled or even absent, sometimes because of study biases (cf. Melfi, 2009). Furthermore, in Carnivora (and perhaps other taxa), research is skewed towards stereotypic over non-stereotypic individuals, especially in enrichment studies (Kroshko, 2015). This biased sampling means that subjects are not a random sample of the overall population, preventing accurate estimates of prevalence and/or true population means.

2.4.3.4 Collecting data by direct observation

Direct observation is ideal for collecting accurate, standardised behavioural data. Furthermore, for stereotypic behaviour, both prevalence and average time budgets can be calculated, since populations can be sampled at random, without biases towards stereotypers. But this data quality comes at a price: direct observation is time-consuming and financially costly, potentially limiting a study's scope. Thus Pomerantz et al. (2013) only assessed 214 individuals (albeit representing 24 species), from just six Israeli zoos. This may introduce noise from individual and site idiosyncrasies and limit their findings' generalisability. A potential solution to this problem, if applied with care, might be to use zoo visitors (e.g. Williams et al., 2012) to collect data across multiple sites and even countries: an approach not yet used in PCM research.

2.4.4 Outcome variable: sources of potential confounds

As mentioned above, outcome variable data can be affected by several sources of noise (non-systematic error), and by biases towards certain species and individuals. Two potential sources of systematic confound can further influence welfare-related variables: extrinsic effects of captive management, and intrinsic differences in pace of life and reproductive strategy.

Extrinsic influences of captive management can clearly affect outcome variables (illustrated in the studbook effects on Ruminant lifespan, for example). In some cases this might add noise to data. For example, Müller et al. (2011) recognised that a potential confound specific to their Ruminantia studies was the selective culling of surplus animals which, if unaccounted for, would artificially reduce species' rLEs. This was handled during data processing by excluding animals that died within two years of birth (so potentially culled). In other cases, management effects may, if they vary systematically across species, potentially create artefactual relationships between intrinsic species-typical attributes and outcome variables (thus Type I errors), or mask real relationships (causing Type II errors). To illustrate with Kroshko et al. (2016)'s Carnivora study, typical housing conditions were found to covary with annual home range size: naturally widely ranging species were often kept in enclosures with little cover. How can one ensure that the home range effect on route-tracing really results from home range size and not this correlated aspect of husbandry? The answer is to include such confounding variables as statistical controls (as these authors did: home range size really does predict route-tracing, even after controlling for the amount of cover: Kroshko et al., 2016). Carefully considering extrinsic effects of captive management during early stages of the research allows appropriate husbandry and environmental data to be collected, or gleaned from publications or survey questions (though one should be aware that there may be 'missed', unmeasured confounding effects, so results should be taken within the context of the variables actually used). One way to then check for potential confounds (cf. Kroshko et al., 2016) is to correlate each husbandry/environmental variable against each species-typical wild attribute (using appropriate PCM tests). Should significant relationships emerge, such confounds can be controlled for by inclusion in subsequent

models. This method is particularly useful for datasets with missing values for different variables. Another approach (cf. Pomerantz et al., 2013) is to include husbandry variables into all hypothesis-testing models (though unless the dataset is complete, this will cause the loss of species with incomplete data).

The second major potential source of confound is intrinsic variation in pace of life and reproductive strategy. For example, simply using infant mortality or reproductive rate as welfare indicators would be naïve since these can reflect intrinsic, evolved differences between species in reproductive strategy (e.g. whether infants are altricial). Using maximum recorded captive lifespan as an outcome variable would also be inappropriate, as lifespan is intrinsically related to body mass (smaller-bodied species tending to have shorter lives than larger species, sensu: Hill, 1950). Therefore, for life history-related outcome variables, evolved intrinsic differences between species must be understood and factored in before inferring any effects of captivity. For example, when Clubb and Mason (2003); Clubb and Mason (2007) found that natural home range sizes predicted captive infant mortality, they then gained data on wild infant mortalities to check that wide rangers did not just naturally have high infant mortalities. Similarly, McDonald Kinkaid (2015) corrected parrots' hatch rates in captivity with wild rates, to control for intrinsic species differences in reproductive rate. Finally, in Müller et al. (2010) and Müller et al. (2011)'s Ruminant work, as we saw, intrinsic life expectancy was controlled for by calculating the ratio of mean lifespan in captivity to the maximum ever recorded for each species. Response to captivity *per se* could then validly be inferred from this derived 'rLE' outcome variable.

2.4.5 Predictor variables: data collection

All the PCM studies described above used published sources (e.g. journals) to obtain values for species-typical values for potential predictor variables: a cost-effective, although quite time-consuming, method. Just as for outcome variables, calculated species-typical values are likely to be more accurate if gleaned from many sources; and researchers should ensure these meet quality criteria based on, e.g., techniques used, representativeness of the wild

populations sampled, data collection time periods, etc (e.g. Clubb and Mason, 2007). Research effort (estimated based on the number of papers published per species) can also be controlled for by including it in statistical models if a potential confound (e.g. for estimates of species-typical innovation rates, see McDonald Kinkaid [2015], following Overington et al., 2009). Once quality data have been compiled, values can then be appropriately summarised to yield a single summary value per species. Note that it is most efficient to collect predictor variable data after the subset of species with good quality outcome data has been identified. However, the collation of predictor variable data should ideally be conducted blind to outcome variable values, to avoid risks of bias.

Textbooks can also yield values for species-typical attributes (cf. Müller et al., 2011; McDonald Kinkaid, 2015) as can books and theses from specialist university libraries. Experts can also be valid sources: they may have unpublished information or be able to provide estimates of species-typical attributes. Furthermore, for some taxa there are freely available databases collating species-typical wild ecology and behaviour from many studies, e.g. Mammalian Species accounts (Mammalogists, 2017) and PanTHERIA (Jones et al., 2009) (see also Ecological Archives: ESA, 2016) Both Kroshko et al. (2016) and Pomerantz et al. (2013) took advantage of such sources. Using these databases is highly time-saving, although inclusion criteria and sources used should be carefully assessed to judge data quality (Bielby et al., 2007; Lemaître et al., 2014).

In some instances, researchers may be unable to find the precise predictor variable data needed to test a hypothesis. For example, despite flight and travel distances being plausible potential risk factors for poor parrot welfare, McDonald Kinkaid (2015) could not find these data. Quantitative data on daily foraging activity budgets of wild Psittaciformes were also scarce. However, based on characteristics of the main food in typical wild diets, and consulting with experts, McDonald Kinkaid (2015) devised a simple, broad categorical descriptor: relatively 'high' or 'low' natural foraging effort, allowing her to investigate relationships between relatively effortful natural foraging and captive welfare. Generating valid predictor variables may thus require some lateral thinking. Finally, while data on

species-typical behaviour and biology are the typical predictors, one study used the discrepancies between wild and captive norms. Pomerantz et al. (2013) collected data on average primate group sizes in zoos and those in the wild to create a 'group size ratio' (captive/wild) predictor. This quantified the degree of mismatch between wild and captive conditions for each species; the greater the mismatch (i.e. smaller values), the more hair-pulling was observed (see Figure 2 in Pomerantz et al., 2013). This could be a useful approach for future welfare PCM researchers to consider.

2.4.5.1 Predictor variables: sources of potential confound

Correlated aspects of species' biology are the main sources of confound for predictor variables. One relevant example is body size, which co-varies with many aspects of most species' life-histories and biology (e.g. Gittleman, 1986). In Carnivora, for example, body size co-varied with home range size (larger-bodied species having larger home ranges). Had analyses naïvely been performed to test the predictive power of home range size alone, body size *per se* could have explained the apparent range size effect. Here, this was managed by including body size in home range size models as a covariate, allowing assessment of home range size effects independently of body size (Clubb and Mason, 2003; Clubb and Mason, 2007; Kroshko et al., 2016). Another example is daily distance travelled and home range size, which both emerged as correlated risk factors for route-tracing. Kroshko et al. (2016) disentangled their effects by including both predictors into the same model, so revealing the apparent daily distance travelled effect to be merely a 'side-effect' of home range size. Ongoing research is now investigating further whether other natural correlates of Carnivora home range (such as metabolic rate) are the true predictors of route-tracing (Bandeli et al., in prep.).

To avoid correlated aspects of species' biology acting as confounds, reading about your species of interest is thus essential, as this pre-warns of interrelated aspects of species' biology. Checking for collinearity between predictor variables within your dataset is also good practice, including any correlates as covariates in final models where appropriate. Another solution might be to run so-called "phylogenetic path analyses" (Hardenberg and

Gonzalez-Voyer, 2013; Gonzalez-Voyer and Von Hardenberg, 2014; van der Bijl, 2017) a topic we outline in Appendix 1.

2.4.6 Data analysis and interpretation

2.4.6.1 Creating the dataset

Microsoft Excel is a good software package for collating data, calculating species' summary statistics, and constructing final comparative datasets (with summary statistics for outcome and predictor variable(s) arranged in columns, and each species in its own row). Microsoft Access is also useful (though more challenging to use) for constructing complex databases, especially for parsing out different types of data from various sources. From these spreadsheets or databases, data can then easily be transferred into statistical packages such as R, Mesquite, etc. (see Appendix 1). Careful data entry checks for errors and outliers should be made throughout all calculations and the final dataset construction.

2.4.6.2 Sourcing phylogenetic trees

All PCM studies require a phylogenetic tree for the species of interest (e.g. Cornwell and Nakagawa, 2017). Effectively a branching diagram depicting hypothesised relationships among species (Baum, 2008) (see Figure 2.2.2), this sums up how closely related – and thus potentially non-independent – the species are. Nowadays, trees are usually built using molecular data (e.g. DNA and protein sequences) (Hall, 2013), though trees based on morphology were historically commonplace (and still have valid use today, especially when incorporating fossil data) (e.g. Wiens, 2004; Zou and Zhang, 2016). For analyses, trees usually need to be in NEXUS or Newick formats, which are readable for PCM software (Felsenstein et al., 1990; Maddison et al., 1997). For most taxa, tree files can be sourced by searching ecological and evolutionary literature, and generally speaking, newer trees are preferable since they reflect the most up-to-date knowledge on relationships between taxa (Arnold et al., 2010). The structure of the tree, and thus relatedness of the species, is then factored in during PCM analyses (as discussed below).

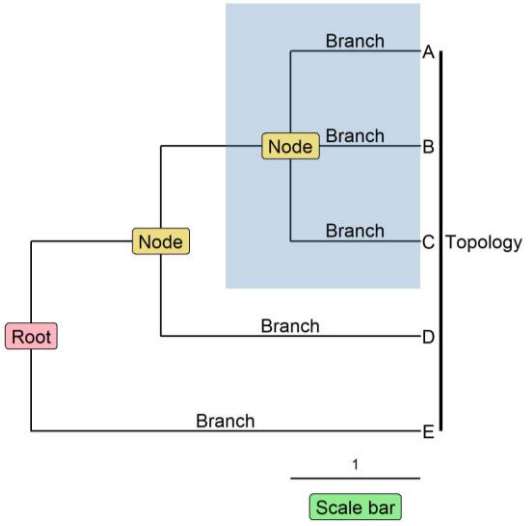

Figure 2.2 Example of a phylogenetic tree (adapted from: McDonald Kinkaid, 2015). This figure depicts a basic tree, a branching diagram depicting hypothesised relationships between these five species, A-E (Baum, 2008). From the base, the 'root' represents a common ancestor from which all species on the tree are descended. A 'node' is a split between branches, representing a speciation event wherein two daughter species (typically) evolve from a parent, ancestral species. Occasionally, three or more daughter species branch from a node: a 'polytomy' (an example is shown here by the species shaded with the blue background). Polytomies can be 'soft', reflecting uncertainty about order of divergence, or 'hard' representing a genuine multiple speciation event (Maddison, 1989). The lines connecting the nodes are 'branches'. When branch 'lengths' are provided, they represent distance in evolutionary time since species spilt (Baum, 2008), also indicated by the scale bar. The ends of the terminal branches are the 'tips' of the tree: each one corresponds to a species, and their ordering and arrangement is the tree's 'topology' (Baum, 2008). The structure of the tree, and thus relatedness of the species, is factored in during PCM analyses (as discussed in the Section 2.4.6).

Trees only display hypothesised relationships between species: when reconstructing historic events, some uncertainty surrounds the precise patterns and/or timings of phylogenetic relationships (sensu Arnold et al., 2010). Consequently, generally no one tree is definitively correct, and trees are constantly being refined to reflect updated knowledge. Nevertheless, PCM statistical tests assume that a given tree's topology and relationships between species are known and correct (Felsenstein, 1985; Garland et al., 2005). Therefore, evolutionary researchers often use consensus trees that sum up agreement between multiple trees (Adams, 1972). Also, it is recommended to perform analyses across a tree 'block' (a set of similar, though slightly different, likely trees, e.g. Arnold et al., 2010). More certain nodes appear more frequently in the block, less certain nodes less frequently, representing

uncertainty in the phylogeny (Arnold et al., 2010). Analyses are then performed across the whole block (with this accounting for topological and branch length uncertainty), so producing robust results for which associated confidence intervals can also be generated (e.g. Arnold et al., 2010; Jetz et al., 2012). Results are then reported, not only as summary values (e.g. median P values and slopes) but also with the 95% confidence intervals for each (e.g. Su et al., 2015). Tree blocks are usually freely available from online literature (e.g. Arnold et al., 2010; Jetz et al., 2012; Jetz et al., 2014; TreeBASE, 2016) with particularly useful exercise files and data from: www.10ktrees.nunn-lab.org/howToUse.html.

2.4.7 Running the statistical analyses

As already outlined, two commonly used PCM statistical tests are PICs and PGLS. Both are extensively reviewed elsewhere, so here we provide brief outlines, highlighting key papers for further reading. Other types of PCM test are also available, depending on specific requirements (Appendix 1 summarising some of these).

Phylogenetic independent contrasts (PICs)

The rationale underlying PICs (Felsenstein, 1985), is that while related species are non-independent, the differences – or contrasts – between them are independent, representing evolution since the species diverged. PICs assume that more recently diverged species (typically those with shorter branch lengths since their last shared node) will be particularly similar to each other, because little time has passed since divergence. In contrast, species diverging long ago (with relatively long branch lengths since their last shared node) are assumed to be less similar to each other, because more time has passed, and more evolution occurred, since divergence. This assumption, which PICs are robust to minor deviations from (Diaz-Uriarte and Garland, 1996), reflects the so-called 'Brownian Motion' model of evolution: one of genetic drift with no selection, simply occurring to a greater extent with the passage of more evolutionary time (sensu Felsenstein, 1985).

PICs handle this as follows. First, for each variable, contrasts are calculated between pairs of species or ancestral nodes. Thus the original set of N non-independent species datapoints are converted to N-1 independent contrasts (see Figure 2.3). Next, each contrast is divided by its standard deviation (the square root of the sum of the relevant branch lengths), to account for how much evolutionary time has passed since divergence (Felsenstein, 1985). These 'standardised contrasts' are now suitable for conventional statistical analysis (e.g. Gittleman and Luh, 1992). Note that because the absolute distance of each contrast from the origin is important, rather than their positions relative to one another, regressions using contrasts should be forced through the origin during analyses (Garland et al., 1992).

Felsenstein (2008) has more recently extended his original PIC method to account for the intra-specific variation discussed earlier (e.g. that caused by sampling error). Values from individuals are used to calculate species-specific means for each attribute, and a weighting factor based on each species' sample size is then incorporated into the contrast calculations.

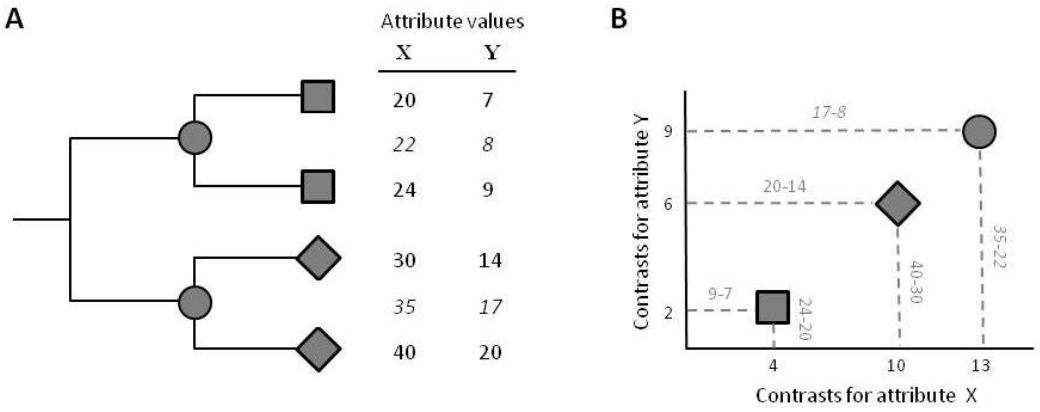

Figure 2.3 Worked example of PICs calculations (from McDonald Kinkaid [2015] who adapted Figure 2 in Clubb & Mason [2004]). In this hypothetical phylogeny (A), squares and diamonds represent extant species, and circles represent their ancestors. Values for two attributes of interest, X and Y, are shown for each species (these are calculated rather than measured directly for ancestors, shown in italics). For a particular attribute, differences between the values of that attribute for pairs of related species represent phylogenetically independent datapoints, or contrasts (e.g., the difference between X values for the pair of species represented by squares is one contrast; and the difference between X values for the pair represented by diamonds is another). As shown in (B), the two sets of contrasts (one for each of the two attributes) can be plotted against each other in order to determine whether the traits are correlated, independent of phylogeny (calculations for each contrast are shown in gray along the dotted lines). In this example, the greater the value of the X contrast, the greater the value of the Y; this suggests the traits are positively correlated. Note that more contrasts would clearly be needed for statistical testing, and that "raw" contrasts like these would need to be standardised by dividing them by their standard deviations (square root of the sum of the branch lengths between the species) before analysis via conventional statistics. The standardisation effectively corrects for the degree of expected phenotypic divergence given the passage of time and a Brownian Motion model of evolution (see Section 2.4.7).

Phylogenetic generalised least squares regressions (PGLS)

PGLS (Grafen, 1989) involves linear regression models that effectively incorporate the tree's topology and branch lengths into the regression equation (Pagel, 1999; Freckleton et al., 2002; Garland et al., 2005). During PGLS, the model estimates how similar species' trait values would be if they evolved by Brownian Motion. The earliest forms of PGLS then incorporated statistical controls for this pattern into each analysis, to 'partial it out' and so prevent it from influencing the final results. In later refinements of PGLS, models assess the extent to which this pattern (i.e. the one expected if traits evolved by Brownian Motion)

actually occurs in the dataset being analysed, in turn allowing this degree of phylogenetic signal to be statistically corrected for. This highlights a major benefit of modern-day PGLS: the generation of a metric termed 'Pagel's Lambda' that captures the degree of phylogenetic signal present (Pagel, 1999; Freckleton et al., 2002; Revell, 2010). Lambda varies from 1 (strong signal, as implied in Brownian Motion) to 0 (no signal, with even close sister species being statistically independent) (Pagel, 1999). When lambda is 1, PGLS thus returns results identical to PICs; when lambda is 0, PGLS performs nearly identically to standard regressions which treat species' datapoints as independent; while at intermediate values, the non-independence between species is corrected for according to the amount of inter-correlation found (Pagel, 1999; Revell, 2010). Thus, PGLS can flexibly control for the actual amount of signal present rather than, as with PICs, assuming strong signal is present.

PGLS can also potentially incorporate different evolutionary models (e.g. by using the R package 'ape': Paradis, 2011). These include: Ornstein-Uhlenbeck, which models 'stabilising selection', wherein attribute evolution is constrained within an optimum range (more realistic for some attributes, e.g. mammalian body size); and other evolutionary patterns, like adaptive radiation, where attributes evolve rapidly immediately after species diverge, slowing towards the tips of the tree (Early Burst: Harmon et al., 2010). Furthermore, intra-specific variation can potentially be incorporated into PGLS models, by providing the standard error associated with attributes' values, or inputting individuals' values for each attribute (Revell, 2012 based on Ives et al., 2007). For further reading, (Symonds and Blomberg, 2014) provide an excellent overview of PGLS.

2.4.8 Presenting and interpreting the results

The results of PCM analyses – test statistics, P values, degrees of freedom, and effect sizes like R^2 – are reported in much the same way as those for other statistical outputs. For PGLS, Pagel's Lambda (Pagel, 1999) should also be reported. Often effect sizes can be rather small, even when models and terms are significant (Freckleton, 2009). Effect sizes should therefore be reported to permit appropriate interpretations of results. Conversely, when sample sizes

are small (N<20, sensu: Blomberg et al., 2003), non-significant results may represent low statistical power rather than truly absent relationships. Additionally, if analyses are performed across a tree block, then results can and should include the associated 95% confidence intervals (which indicate the ranges within which true values likely lie).

Visual representations, such as graphs of correlations between attributes, are also useful. They can provide visual information, not just on effect sizes and the explanatory value of predictor variables, but also on potential outliers, and on thresholds that may exist (below which species have no apparent welfare problems, but above which signs of poor welfare are clear). However, because graphs from PIC models use contrast values rather than species' values, axes values will be somewhat arbitrary and non-informative (despite accurately depicting relationships). Alternatively, species' values may be plotted on the relevant axes as per standard regressions. This will not illustrate the PCM statistics run (as should be stated in figure legends), but is more intuitive to understand. Researchers using PGLS should ensure they plot the PGLS regression line, which will be 'weighted' appropriately to that particular analysis (Symonds and Blomberg, 2014).

By validly testing hypotheses to identify risk and protective factors, PCM results can be interpreted in three main ways to improve animal welfare. First, they can identify vulnerable 'problem' species to target for special care. Second, the principles they yield can help predict which additional species beyond those in the dataset, are likely, or not, to be at risk of health and welfare problems. Third, they can generate novel ideas about how to improve husbandry (e.g. via altering species' typical diets or enclosure characteristics). Such manipulations can also test the causality of relationships. PCM outputs merely represent correlations between wild biology predictors and welfare-relevant outcomes: even after carefully considering the various correlates of predictor variables and systematic confounds of outcome variables, and performing 'path' analyses (Appendix 1), true causality cannot be assumed (sensu Gittleman, 1989; Garland et al., 2005). But PCM outputs do yield causal hypotheses, which can potentially be tested experimentally. PCMs can thus inform future

work that uses the other two complementary approaches to welfare research, the results of which can help to both test causal hypotheses and improve animal husbandry.

2.5 Discussion

Many members of wild and semi-wild species are housed in contexts as diverse as farms and domestic homes (Mason et al., 2013), and results from PCMs could be relevant to all of them if applied by aquaculturalists, aviculturalists, and others. However, PCMs are particularly useful for zoos and aquaria for the following reasons: these institutions actively aim to promote animal welfare in evidence-based ways; much research has already been conducted on zoo animals, making existing theses and publications ripe for collation and meta-analysis; zoos have already collected vast amounts of welfare-relevant data (e.g. via ZIMS), the incredible value of which has barely been harnessed; and finally, the size and diversity of global zoological collections (Conde et al., 2011) gives potential for impressive statistical power (sensu Blomberg et al., 2003). Zoo researchers are thus enviably positioned to capitalise on PCM-based research. It must be recognised that applying PCMs can be technically daunting: good trees must be sought and potentially complex statistical analyses performed. But many helpful resources are readily available: papers and books (we particularly recommend Arnold et al., 2010; Freckleton, 2009; and Symonds and Blomberg, 2014); online lecture notes, primers, and forums; software support; and experts in many universities' biology, ecology, and zoology departments. Furthermore, the benefits of running PCMs to investigate welfare issues are worth the effort.

For one, PCMs represent an economical, efficient complement to experimentation and epidemiology – the traditional methods for studying zoo animal health and welfare. Using the published literature alone, we found nearly 20 untested hypotheses that are ideal for testing using PCMs (Table 2.1), with many more possible beyond these. Furthermore, PCMs can address welfare research questions that would be logistically or ethically impossible to investigate in other ways (cf. Clubb and Mason, 2004; Clubb and Mason, 2007). Such questions include whether being an ecological specialist, or unable to hunt, migrate, or fly,

compromises welfare in captive animals, and whether prey animals have evolved to mask states of pain or sickness from potential predators. PCMs are unique in making these fundamentally fascinating and practically important questions amenable to study.

Second, just like other methods of investigating welfare issues, PCM results can indicate effective ways in which to improve husbandry; but because they can also address questions hard to tackle via experimentation or epidemiology, the insights they yield can be novel. As reviewed above, PCMs have thus generated evidence-based recommendations to supply carnivores with more variety and control, in order to reduce route-tracing; to provide ruminants that browse in the wild with more natural diets in captivity, in order to reduce nutrition-related mortality; to protect female ruminants, especially Cervidae, from rutting males in order to reduce seasonal deaths; to house zoo primates in naturalistic group sizes, and encourage active travel, in order to reduce two forms of abnormal behaviour; and to supply captive parrots with more naturalistic diets, along with opportunities to learn and problem-solve, in order to enhance their welfare. Furthermore, by identifying the most 'susceptible' species (cf. Pomerantz et al., 2013), such as ruminant species with the lowest rLEs (Müller et al., 2011), PCMs can highlight those it might be most important to target for improvements.

A third major benefit of using PCMs to investigate welfare issues is that the data collated and results generated could have great benefits for global collection planning. PCMs, as we have seen, can identify both specific species intrinsically unlikely to thrive in zoo conditions, and also broad types of species at risk of welfare problems. While one response may be to target such species for special care, an alternative is to phase them out in favour of species revealed to be intrinsically likely to thrive in zoo conditions and protected from welfare problems. Such recommendations may be negatively received by some in the zoo community, but we propose that factoring animal welfare into collection planning is both strategic and practical (see Table 2.2). Of the 4,000 terrestrial vertebrate species currently represented in zoos, many are in populations too small to be viable (Lees and Wilcken, 2009; Conde et al., 2013). Furthermore, zoos have limited spatial and financial resources

(Lees and Wilcken, 2009; Fa et al., 2011; Conde et al., 2013; Gusset et al., 2014; McGowan et al., 2017). It is thus important to decide which species zoos should focus on (Fa et al., 2011; Conde et al., 2013; Gusset et al., 2014). Endangeredness has been proposed as one criterion, but in reality, diverse factors are currently at play in collection planning (Fa et al., 2011; Bowkett, 2014). If species-typical welfare explicitly played a role in such decisions, the benefits would range from practical and economic advantages to improvements in the viability and conservation relevance of captive populations (e.g. due to reduced rates of domestication) (see Table 2.2). PCMs could thus be part of a holistic approach involving evidence-based, welfare-guided collection planning, with the ultimate goal of ensuring that all captive populations can readily be kept successfully (e.g. Conde et al., 2013; Gusset et al., 2014; Alroy, 2015; Kaumanns and Singh, 2015).

Table 2.2 Benefits of factoring species-typical captive welfare into collection planning: a potentially valuable role for PCMs (from: Mellor et al., 2018b).

Type of benefit	How achieved	Why important
Improved animal welfare	Phasing out species prone to poor welfare; prioritising species prone to good welfare	WAZA recommends that zoos should meet animals' behavioural and physical needs (Fa et al., 2011; Mellor et al., 2015). Some welfare problems (e.g. manifest in stereotypic behaviour and infant mortality) negatively affect public perception (e.g. Miller, 2012)
Efficient use of space, funds, and other resources	Prioritising species already pre-disposed to good welfare, obviates needs for extensive research or resource allocation into improving welfare	Zoos have limited space and funds (e.g. Lees and Wilcken, 2009; Fa et al., 2011; Conde et al., 2013; Gusset et al., 2014; McGowan et al., 2017)
Easy to maintain viable, self-sustaining populations	Species intrinsically prone to good welfare can readily be held in many zoos, and easily achieve large effective populations sizes and self-sustainability	Large effective population sizes are important for genetic viability (e.g. Lees and Wilcken, 2009; Fa et al., 2011; Conde et al., 2013); captive populations should also be net sources of animals, not net sinks (e.g. Clubb et al., 2009; Fa et al., 2011; McGowan et al., 2017)
Reduced domestication	Species in which most individuals successfully reproduce are under weaker selection pressures than species in which only a small fraction of individuals do	If the population kept in zoos are to represent those in the wild, genetic adaptation to captivity is undesirable (O'Regan and Kitchener, 2005; McDougall et al., 2006; Fa et al., 2011)

Chapter 3: Route-tracing in captive Carnivora: is foraging niche a risk factor?

Abstract

Species from the diverse order Carnivora ('carnivores') are popular in zoological collections. Route-tracing, i.e. repetitively following a set route or path within the enclosure, is rare in some of these species, yet common and time-consuming in others. Restriction of the appetitive phase of hunting, i.e. the search and pursuit of prey, has been previously hypothesised to explain route-tracing by some captive carnivores. However, support for this is mixed. My main aim of this chapter was to test the following hunting-related hypotheses: i) that route-tracing is redirected hunting, emerging because hunting is restricted in captivity; ii) that restricting pursuit hunters leads to route-tracing; and iii) that restrictions on hunting relatively large prey leads to route-tracing. My secondary aim was to investigate whether these foraging niche variables explained any variance in route-tracing not explained by a known biological risk factor for it: annual home range sizes. Using phylogenetic generalised least squares regressions to control for species relatedness, I therefore explored relationships between species-typical foraging niche (reliance on self-hunted meat, kill and hunt rates, hunting strategy, chase distance, and relative prey size) and my outcome: species-typical median % observations route-tracing. Values for the latter comprised of 459 representatives from 27 species held in zoos worldwide, calculated from data held in the Captive Carnivore Database. No aspect of foraging niche significantly predicted route-tracing, but there was a trend for species most reliant on self-hunted meat to route-trace the most. However, this trend disappeared once annual home range sizes was included in the model. In sum, my data did not support any of my hypotheses, and no aspect of wild foraging niche explained any of the variance in route-tracing not explained by

annual home range sizes. My findings therefore imply that for captive hunters, relinquishing hunting does not lead to route-tracing. Based on my results and the Captive Carnivore Database itself I describe areas for future research, both species- and family-specific. Finally, I propose that easily implemented standardisation of reporting within published zoo-based studies would improve their scientific value; better facilitate future meta-analytical studies; and, ultimately, improve welfare across this charismatic taxonomic group and others.

3.1 Introduction

Species from the diverse order Carnivora ('carnivores' from herein) are popular in zoological collections. Route-tracing, i.e. repetitively following a set route or path within the enclosure, is relatively rare in some carnivore species, e.g. raccoons, *Procyon lotor* (Boorer, 1972), and black bears, *Ursus americanus* (Clubb and Mason, 2007). However, other species are far more prone to route-tracing, and individuals may devote large amounts of their daily activity budget doing so, e.g. polar bears, *U. maritimus*, and fossa*, Cryptoprocta ferox* (Dickie, 2005; Clubb and Mason, 2007). Route-tracing and other stereotypic behaviours are management problems for zoos, because they are indicative of compromised welfare (Mason, 2006b), are perceived negatively by the public (Miller, 2012), and affected animals may also suffer breeding problems (e.g. stereotypic male American mink, *Neovison vison*, win fewer matings: Díez-León et al., 2013). The latter directly affects the likelihood of maintenance of large, self-sustaining populations: one the main goals of modern zoos (Section 1.2). Understanding why some carnivore species are so prone to route-tracing, therefore, is fundamentally important in managing captive carnivore populations.

Across the Carnivora, diverse species-typical foraging behaviours are observed (van Valkenburgh and Wayne, 2010). For instance, some species are hypercarnivorous (Holliday and Steppan, 2004; Solé and Ladevèze, 2017) – >70% of the diet consisting of the flesh of other animals (van Valkenburgh, 1988) – such as the fossa (Lührs and Dammhahn, 2010), and lion, *Panthera leo* (Schaller, 2009). Not all carnivores are so carnivorous though. Giant and red pandas*, Ailuropoda melanoleuca* and *Ailurus fulgens*, are herbivorous – i.e. consume plant-matter – and these mainly eat bamboo (Chorn and Hoffmann, 1978; Zhang et al., 2009). Omnivorous carnivore species include the fennec fox, *Vulpes zerda* (Brahmi et al., 2012), and brown bear, *Ursus arctos* (Stenset et al., 2016), which consume a range of plant and animal matter. Species that do eat meat differ in reliance on hunting to get that meat: some eat large quantities of carrion e.g. wolverines, *Gulo gulo* (Magoun, 1987; van Dijk et al., 2008), and brown hyaenas, *Parahyaena brunnea* (du Bothma, 2010); whereas others like the caracal, *Caracal caracal*, and cheetah, *Acinonyx jubatus*, are far more reliant on hunting live prey (du Bothma, 2010). Within hunting species, hunting 'styles' also vary. Ambush

predators like jaguar, *P. onca*, and puma, *Puma concolor*, typically stalk and use powerful, heavy forelimbs to grapple with and subdue their prey (van Valkenburgh, 1985). Cursorial, pursuit predators chase down their prey, in some cases over large distances (van Valkenburgh, 1985) e.g. grey wolf, *Canis lupus*, and/or with high speed and agility e.g. cheetah (Wilson et al., 2013). Semifossorial species such as badgers, *Meles meles*, dig for their prey. Behaviours associated with successfully finding food, such as hunting, are a fundamental necessity for all these species; therefore, animals are highly motivated to perform them.

The foraging and feeding environment a captive animal experiences is often very different from that in which the species has evolved (see Section 1.3). Captive meat-eaters are almost always given carrion, essentially, which for species adapted to hunt live prey could result in frustrated motivation to hunt (Clubb and Vickery, 2006). This type of mismatch, i.e. between how a species has evolved to behave, and the behaviour the captive environment allows individuals to perform, can affect welfare (Section 1.1 and cf. Koene, 2013; Mason et al., 2013). For example, McDonald Kinkaid (2015) found parrot species whose wild diets require extensive (*versus* quick) search had more prevalent self-directed feather-damaging behaviour in captivity (also see Chapter 4), and difficulties in providing appropriate browse to captive browsing ruminants means they have reduced life expectancy when compared with grazers (Müller et al., 2011). As I discuss next, given that hunting, for some species, is critical for survival in the wild, and hunting-related behaviours persist in captivity even when food is freely available, the mismatch between motivation and ability to fulfil that motivation may explain some of the variation in species differences in route-tracing across captive carnivores.

Restriction of the appetitive phase of hunting, i.e. the search and pursuit of prey, has been previously hypothesised to explain welfare problems in captive carnivores (e.g. Mason and Mendl, 1997; Clubb and Vickery, 2006). Indeed, hunting might be considered a behavioural 'need' in some carnivores. Firstly, successful hunting is often crucial for survival in the wild, and is behaviourally persistent despite failures (e.g. Smith, 1980; Holekamp et al., 1997), its

time and energy costs, and inherent risks i.e. the carnivore's own injury or death (Caro, 2017). Secondly, even when satiated, some animals still hunt (e.g. domestic cats, *Felis catus*, will hunt despite being well-fed: Adamec, 1976; Dauphiné and Cooper, 2009). Like hunting, route-tracing usually has a temporal relationship with feeding, being most intensive before feeding and usually ceasing afterwards (Mason, 1993; Weller and Bennett, 2001; Vickery and Mason, 2004). Route-tracing is more prevalent in the Carnivora than other mammalian orders (Mason et al., 2007), and has been proposed to represent frustrated attempts to hunt (Mason, 1993). Further to this, foraging-related environmental enrichments that mimic certain aspects of hunting, e.g. chase, often successfully reduce route-tracing (e.g. Markowitz and LaForse, 1987; Forthman et al., 1992; Shepherdson et al., 1993). A recent comparative study investigating risk factors for carnivore welfare also yielded a link between pursuit hunting styles and route-tracing. Kroshko et al. (2016) reported that species with the longest chase distances in the wild performed the most route-tracing in captivity, as do those with large annual home range sizes (the latter in agreement with: Clubb and Mason, 2003; Clubb and Mason, 2007; with a similar trend reported in: Miller et al., 2018). Additionally, there are indications prey selection might affect route-tracing, as larger-bodied carnivores perform the most intensive route-tracing (Clubb and Mason, 2003; Clubb and Mason, 2007; Kroshko et al., 2016). The importance of this finding is that body size also determines prey selection – at ~20kgs, carnivore species switch from selecting relatively small to relatively large prey (Carbone et al., 1999; Carbone et al., 2007).

However, support for frustrating hunting leading to route-tracing in captive carnivores is not unequivocal. Some wild animals choose to scavenge 'free meat' from human snares (Knopff et al., 2010; Jacobson et al., 2016) and from other predator's kills rather than to hunt. Additionally, captive animals may route-trace at times other than pre-feeding (e.g. during the mating season: Carlstead and Seidensticker, 1991; and in response to aversive events, e.g. during social stress: Kolter and Zander, 1997). Whilst route-tracing, some captive animals also perform other behaviours incompatible with successful prey capture, e.g. vocalisations, which is at odds with the notion that route-tracing represents redirected hunting (squeaking by American mink, *Neovison vison*, and meowing by African wild cats, *Felis silvestris lybica*: Mason, 1993; Nicastro, 2004). In contrast to Kroshko et al. (2016)'s

chase distance finding mentioned above, another Carnivora comparative study did not find route-tracing to be explained by restriction of hunting, instead reporting large annual home range sizes to be the driver (Clubb and Mason, 2003; Clubb and Mason, 2007). Given the mixed support just discussed, that Kroshko et al. (2016)'s chase distance result requires replication (being based on five species, far fewer than the ≥20 species minimum recommended, see Chapter 2 and: Blomberg et al., 2003), and the availability of new sources of wild carnivore dietary information (e.g. Wilman et al., 2014), there is scope to further examine the relationship foraging niche, specifically hunting, has with route-tracing across the Carnivora.

Based on what I review above, in this chapter I test the following hypotheses:

i. Route-tracing is re-directed hunting emerging because hunting is restricted in captivity
   → *Prediction*: species that are most reliant on hunting in the wild should spend the most time route-tracing in captivity
ii. Restricting pursuit hunters leads to route-tracing in captivity
   → *Prediction:* species that use chase to capture their prey should spend the most time route-tracing in captivity
iii. Restrictions on hunting relatively large prey items leads to route-tracing in captivity
   → *Prediction*: species that hunt relatively large prey in the wild should spend the most time route-tracing in captivity

As mentioned above, large annual home range sizes predicts route-tracing across carnivores (Clubb and Mason, 2003; Clubb and Mason, 2007; Kroshko et al., 2016; with a similar trend reported in Miller et al., 2018). Therefore, a secondary aim of this chapter is to investigate whether foraging niche might explain any of the variance in route-tracing *not* explained by annual home range sizes.

3.2 Methods

3.2.1 Outcome variable: route-tracing data collection and the Captive Carnivore Database

My outcome variable was species-typical median % observations spent route-tracing in captivity by affected animals (see Section 3.2.1 for rationale). As detailed in Section 1.2.2, stereotypic behaviours such as route-tracing are management problems and validated, stress-sensitive welfare indicators (but prone to false negatives as some animals become inactive instead: Fureix and Meagher, 2015; Fureix et al., 2016).

A colleague, Miranda Bandeli, and I updated an extensive database of behaviour and corresponding living conditions of captive carnivores, collated via systematic searches of published observational studies. The Captive Carnivore Database has formed the basis of two doctoral theses – including the current one – and two Masters theses to date (Clubb and Mason, 2003; Clubb and Mason, 2007; Kroshko et al., 2016; Bandeli, 2018). Briefly, data collection methods were as follows. Covering years 1960 – 2016 inclusive, papers from specific journals were systematically searched using species' scientific and common name(s) as criteria (see Table 3.1 for species names and Table 3.2 for journals). For the current database update, we also made the same searches of suitable theses published online by the British Library (EThOS, 2017), and I also collected some data opportunistically from researchers presenting appropriate work at conferences. For papers meeting our quality inclusion criteria (described next) reported stereotypic behaviour values and any corresponding rearing, husbandry and/or demographic data were entered into the Captive Carnivore Database. Stereotypic behaviours were categorised according to outward form: 'route-tracing' (repetitively following a fixed path or route); 'stationary' (performed on the spot, e.g. head-rolling, weaving, and rocking etc.); and 'oral' (involving the mouth, e.g. paw sucking, bar-biting, fur chewing).

Table 3.1 Species included in each version of the Captive Carnivore Database (Y=that species was included in a given version). Species' scientific and common names detailed here were used as search terms during literature searches. 'Clubb version' refers to the first version of the Captive Carnivore Database, created in 1999 by Ros Clubb; 'Kroshko version' refers to the 2010 update made by Jeanette Kroshko. The number of individuals (N) per species included in the most recent version of the database is also provided.

Species scientific name	Common name	Clubb version	Kroshko version	Current version	Final Ns
Acinonyx jubatus	Cheetah	Y	Y	Y	183
Ailuropoda melanoleuca	Giant panda	Y	Y	Y	14
Ailurus fulgens	Red panda			Y	31
Arctocephalus pusillus	Cape fur seal			Y	2
Canis latrans	Coyote		Y	Y	20
Canis lupus	Grey wolf		Y	Y	18
Caracal caracal	Caracal	Y	Y	Y	11
Catopuma temminckii	Asian golden cat		Y	Y	5
Cryptoprocta ferox	Fossa			Y	14
Eumetopias jubatus	Steller sea lion		Y	Y	7
Felis chaus	Jungle cat	Y	Y	Y	3
Felis margarita	Sand cat	Y	Y	Y	11
Felis nigripes	Black-footed cat		Y	Y	2
Felis silvestris	Wildcat	Y	Y	Y	2
Genetta tigrina	Cape genet	Y	Y	Y	1
Gulo gulo	Wolverine			Y	3
Halichoerus grypus	Grey seal		Y	Y	12
Helarctos malayanus	Sun bear		Y	Y	39
Leopardus colocolo	Colocolo		Y	Y	2

Species scientific name	Common name	Clubb version	Kroshko version	Current version	Final Ns
Leopardus geoffroyi	Geoffroy's cat	Y	Y	Y	12
Leopardus pardalis	Ocelot	Y	Y	Y	26
Leopardus tigrinus	Oncilla cat			Y	8
Leopardus wiedii	Margay	Y	Y	Y	5
Leptailurus serval	Serval	Y	Y	Y	21
Lontra canadensis	North American river otter		Y	Y	130
Lontra longicaudis	Neotropical otter		Y	Y	2
Lynx canadensis	Canada lynx	Y	Y	Y	6
Lynx lynx	Eurasian lynx	Y	Y	Y	10
Martes flavigula aterrima	Yellow-throated marten			Y	6
Martes foina	Beech marten		Y	Y	38
Melursus ursinus	Sloth bear	Y	Y	Y	6
Nasua nasua	South American coati		Y	Y	4
Neophoca cinerea	Australian sea lion		Y	Y	2
Odobenus rosmarus	Walrus		Y	Y	4
Otocolobus manul	Pallas' cat		Y	Y	7
Neovision vison	American mink	Y	Y	Y	1310
Panthera leo	Lion	Y	Y	Y	56
Panthera onca	Jaguar	Y	Y	Y	25
Panthera pardus	Leopard	Y	Y	Y	72
Panthera tigris	Tiger	Y	Y	Y	111
Parahyaena brunnea	Brown hyena	Y	Y	Y	2

Species scientific name	Common name	Clubb version	Kroshko version	Current version	Final Ns
Phoca vitulina	Harbour seal		Y	Y	10
Potos flavus	Kinkajou	Y	Y	Y	1
Prionailurus bengalensis	Leopard cat	Y	Y	Y	4
Prionailurus viverrinus	Fishing cat	Y	Y	Y	5
Puma concolor	Cougar	Y	Y	Y	12
Puma yagouaroundi	Jaguarundi		Y	Y	11
Suricata suricatta	Meerkat	Y	Y*		-
Tremarctos ornatus	Spectacled bear	Y	Y	Y	3
Uncia uncia	Snow leopard	Y	Y	Y	27
Ursus americanus	American black bear	Y	Y	Y	5
Ursus arctos	Brown bear	Y	Y	Y	62
Ursus maritimus	Polar bear	Y	Y	Y	89
Ursus thibetanus	Asiatic black bear	Y	Y	Y	95
Vulpes lagopus	Arctic fox	Y	Y	Y	54
Vulpes vulpes	Red fox	Y	Y	Y	27
Vulpes zerda	Fennec fox		Y	Y	8

* Meerkat was erroneously included in the first two versions, but excluded in the current one as stereotypic behaviour values for this species featured juveniles: an exclusion criterion (see Section 3.2.1)

Prior to our update, we checked through the entire database for errors. A very small number of entries contained minor errors (erroneous inclusion of juveniles, and some small calculation errors), which were corrected (see Appendix 2 for a list of these).

Captive Carnivore Database: quality inclusion criteria

For inclusion into the Captive Carnivore Database, studies had to meet certain quality criteria. These controls are very similar to those of Clubb and Mason (2003, 2007) and are identical to those of Kroshko et al. (2016), with two minor differences between the two highlighted below.

Firstly, studies had to focus on captive wild animals, i.e. domesticated species such as dogs, *Canis lupus familiaris*, and cats were excluded. The minimum data collection period was 1 day; reduced from 1 week as per Clubb and Mason (2003, 2007), because many studies of captive animals are short in time frame. Studies were excluded if they used inconsistent data collection methods; if they did not define stereotypic behaviour; if they focused only on periods of high stereotypic behaviour (which would likely over-inflate estimates); and/or if animals were selectively bred for decreased stereotypic behaviour (only relevant to farmed mink and foxes and a criterion introduced by Kroshko et al. [2016]). Additionally, studies had to feature ≥ 1 adult animal (data for sub-adult individuals were excluded from subsequent analyses). To avoid short-term disturbance effects, studies were also excluded if animals were food-restricted or undergoing a husbandry change (such as a birth, or enclosure move). For a similar reason, of the enrichment studies that met our quality criteria, only baseline data (i.e. pre-enrichment data) only were included.

Table 3.2 Details of the journal titles and other published sources searched for observational studies of captive carnivore behaviour. At the time of writing, abstracts from the International Conference on Environmental Enrichment were only available up until 2007. Likewise, Shape of Enrichment publications were only available up until 2012.

Source/journal title (ISSN/link to website)	Clubb version	Kroshko version	Current study
Zoo Biology (1098-2361)	1960-1999	2000-2010	2011-2016
International Society for Applied Ethology (ISAE) abstracts	1960-1999	2000-2010	2011-2016
International Zoo Yearbook (1748-1090)	1960-1999	2000-2010	2011-2016
Shape of Enrichment (theshapeofenrichmentinc.wildapricot.org)	-	1992-2010	2011-2012
International Conference on Environmental Enrichment, abstracts	-	2001-2007	-
Animal Welfare (0962-7286)	-	1992-2010	2011-2016
Applied Animal Behaviour Science (1872-9045)	-	1984-2010	2011-2016
Journal of Applied Animal Welfare Science (1088-8705)	-	1998-2010	2011-2016
British Library EThOS	-	-	1960-2016

3.2.2 Data processing and calculations of species medians for route-tracing

Processing the 2016 update of the Captive Carnivore Database

Forty-eight studies were added to the Captive Carnivore Database during the current update. The database now contains data on stereotypic behaviour, and some on rearing history and current living conditions, for 2,656 individuals from 56 species held in zoos worldwide. I then processed the dataset as follows. As my focus was on route-tracing, I excluded observations of other forms of stereotypic behaviour (in practise, these were rarely encountered within the database). Following Clubb and Mason (2003, 2007) and Kroshko et al. (2016), animals which did not route-trace were also excluded, necessary because there is research bias towards stereotypic animals, making calculation of population prevalence or time budgets impossible (also see Sections 2.4.3 and 7.3). After these exclusions, I had route-tracing data from 510 animals from 48 species.

A minority of animals (~198) were part of more than one study. To avoid pseudoreplication and following Kroshko et al., (2016), I calculated an individual's mean % observations spent route-tracing across the relevant studies, then calculated a mean across all individuals' means to yield a single value (study mean % observations spent route-tracing) representing these animals and studies. A worked example is shown in Table 3.3. Note that all animals in these studies were included in the final study mean, even if they did not feature in all the studies.

For each species in turn, using data from affected individuals I calculated study means for % observations spent route-tracing (see also the paragraph immediately above and Table 3.3), followed by a median across study means to yield species-typical median % time route-tracing (medians are preferred for summary statistics to reduce the effects of outliers: Gittleman, 1989). Incorporating intra-specific variation into analyses by giving standard

errors associated with summary statistics, or by using values from individuals is recommended by some (see Ives et al., 2007; Garamszegi and Møller, 2010; Hansen and Bartoszek, 2012). However, this was not possible for my study, as rather than reporting individual-level values for route-tracing, some studies instead reported only study means. Therefore, to ensure representativeness of species datapoints, my final step was to exclude species represented by fewer than five route-tracers (following e.g. McDonald Kinkaid, 2015; Kroshko et al., 2016). Thus, the final dataset used for analyses comprised route-tracing data for 459 individuals from 27 species (see Table 3.5 for species-typical median % observations route-tracing values), along with some corresponding rearing and husbandry data. Appendix 3 displays species-typical median route-tracing values of the 51 species whose route-tracing status was known for all representatives, including those with fewer than five individuals.

Table 3.3 In this hypothetical example, three different studies provide route-tracing values (% observations [obs.]) for four fossa who feature one or more of the studies. Dashes indicate a fossa did not feature in a given study. To avoid pseudoreplication, individual means for route-tracing are calculated across these studies (shown in italics), and a mean of means calculated across these (shown in bold). Later, this single value (study mean % time spent route-tracing) is used for calculation of species median % time spent route-tracing (see Section 3.2.2 for more details).

Animal	Study A	Study B	Study C	% obs. route-tracing
Fossa 1	3%	4%	0%	*2.33%*
Fossa 2	10%	8%	-	*9%*
Fossa 3	12%	11%	15%	*12.67%*
Fossa 4	-	-	6%	*6%*
		Mean of individual means =		**7.5%**

3.2.3 Predictor variable data collation

Wild foraging niche predictor variables associated with each hypothesis, with justification and sources, are as follows (all values are shown in Table 3.5):

i. Route-tracing is re-directed hunting hypothesis: predictors

a. Reliance on self-hunted meat

Percentage (range: 0-100%). This variable describes a species' reliance on hunting for its meat. I collated data on species-typical reliance on self-hunted animal matter from information given on the use of 10 dietary categories reported in the mammalian EltonTraits foraging database (Wilman et al., 2014). I summed across dietary categories recorded in this database relevant to my hypothesis, namely use of invertebrates and vertebrates, which yielded my predictor variable (percentage reliance on self-hunted dietary meat). Note: I did not include reliance on scavenged material (i.e. carrion) as I was only interested in meat that the species typically hunts for itself.

If my data support this hypothesis, I expect species most reliant on self-hunted meat, and so presumably most motivated to hunt, to route-trace the most. Data were available for 27 species.

b. Hunt rate

Median hunts recorded (/24hrs). Within hunting species, this variable is the species-typical median number of hunts recorded within 24 hours, a reflection of hunting motivation. Calculated from the Wild Carnivore Behaviour Database (see Section 3.2.4).

If my data support this hypothesis, I expect species that hunt most frequently to route-trace the most. Data were available for 8 species.

c. Kill rate

Median kills recorded (/24hrs). This variable's assumptions and source are as per hunt rate but is instead the number of kills.

If my data support this hypothesis, I expect species that kill most frequently to route-trace the most. Data were available for 10 species.

ii. Restricting pursuit hunters leads to route-tracing hypothesis: predictors

a. Hunting strategy

Categorical with two levels (pursuit *versus* non-pursuit). Species were classed as either mainly using *pursuit* or *non-pursuit* hunting styles, taken from van Valkenburgh (1985) with some re-classifications by Janis and Figueirido (2014). *Pursuit* included species that used pursuit (a chase usually >500m, rarely preceded by stalking) and pounce/pursuit (moving search ending in a pounce or chase) hunting styles (van Valkenburgh, 1985). *Non-pursuit* included ambush species (a short distance rush usually <500m, frequently preceded by a stalk) and those that rarely hunt at all (van Valkenburgh, 1985). Based on forelimb morphology and knowledge of hunting behaviour, cheetah was re-classified as pursuit (Janis and Figueirido, 2014) rather than ambush as per van Valkenburgh (1985), being more specialised for pursuit than other felids. Likewise, serval, *Leptailurus serval*, caracal, and Canada lynx, *Lynx canadensis*, were re-classified as pounce/pursuit, being more alike cursorial pounce/pursuit canids (Janis and Figueirido, 2014) than other ambushing felids as per van Valkenburgh (1985). For two further species, I contacted notable field experts to request classification of their species of interest. Thus, fossa was classified as pursuit (M. Lührs, pers. comm., 2017), and Pallas' cat, *Otocolobus manul*, as ambush (S. Ross, pers. comm., 2017).

If my data support this hypothesis, I expect pursuit style predators to route-trace the most. Data were available for 17 species.

b. Chase distance

Median chase distance recorded (range: 13.71-240m). Within hunting species, the distance travelled from the beginning of a chase until either the predator gave up or caught and killed the prey. Calculated from the Wild Carnivore Behaviour Database (see Section 3.2.4).

If my data support this hypothesis, I expect species with the longest chase distances to route-trace the most (as found by: Kroshko et al., 2016). Data were available for 9 species.

iii. Restrictions on hunting relatively large prey items leads to route-tracing hypothesis: predictors

a. Relative prey size

This is the ratio between the body mass of the most common prey item hunted by a carnivore species, and the body mass of the carnivore itself. As mentioned in Section 3.1, body size both predicts route-tracing (larger-bodied species route-trace the most: Clubb and Mason, 2004; Clubb and Mason, 2007; Kroshko et al., 2016) and wild prey selection (most carnivore species larger than ~20kgs select larger prey: Carbone et al., 1999; Carbone et al., 2007). Species-typical body masses came from PanTHERIA database (Jones et al., 2009), and body masses of the most common prey item taken by each species were taken from Carbone et al. (2014). The ratio between these quantifies prey selection: larger values represent selection of relative larger prey items, and vice versa.

If my data support this hypothesis, I expect species that hunt relatively large prey to route-trace the most. Data were available for 22 species.

3.2.4 Updating the Wild Carnivore Biology Database

As mentioned in the previous Section (3.2.3) the Wild Carnivore Behaviour Database was a source for some of my predictor variables. Miranda Bandeli and I updated this database, following Clubb and Mason (2003; 2007) and Kroshko et al. (2016). Briefly, we systematically searched through eighteen journals (see Table 3.4) previously identified by Clubb and Mason (2003; 2007) as commonly publishing papers containing information on carnivore ecology, using the species names listed in Table 3.1 as search terms. Papers from other journals containing relevant data were also incorporated when encountered, as was correspondence from field experts.

Table 3.4 Details of the journals systematically searched for data on wild carnivore behaviour for inclusion into the Wild Carnivore Behaviour database. Note that the years searched vary for some according to availability and the journals' own publication dates.

Source/journal title (ISSN)	Clubb version	Kroshko version	Current study
Acta Theriologica (0001-7051)	1960-1996	2000-2010	2010-2016
African Journal of Ecology (0141-6707)	1962-1999	2000-2010	2010-2016
Arctic (004-0843)	1960-1999	2000-2010	2010-2016
Biological Conservation (006-3207)	1968-1999	2000-2010	2010-2016
Canadian Field-Naturalist (0008-3550)	1960-1991	2000-2010	2010-2016
Canadian Journal of Zoology (008-4301)	1967-1999	2000-2010	2010-2016
Journal of Animal Ecology (0021-8790)	1960-1999	2000-2010	2010-2016
Journal of Mammalogy (0022-2372)	1960-1999	2000-2010	2010-2016
Journal of Zoology (1469-7998)	1960-1999	2000-2010	2010-2016
Journal of Wildlife Management (0022-541X)	1960-1997	2000-2010	2010-2016
Mammal Review (0305-1838)	1970-1999	2000-2010	2010-2016
Mammalia (0025-1461)	1960-1999	2000-2010	2010-2016
Oecologia (0029-8549)	1969-1999	2000-2010	2010-2016
Oikos (1600-0706)	1960-1999	2000-2010	2010-2016
South African Journal of Wildlife Research (0379-4369)	1971-1978	2000-2010	2010-2016
South African Journal of Zoology (1562-7020)	1979-1999	2000-2010	2010-2016
Wildlife Monographs (0084-0173)	1960-1996	2000-2010	2010-2016
Zeitschrift für Säugetierkunde (1616-5047)	1960-1999	2000-2010	2010-2016
British Library EThOS	-	-	1960-2016

Note that the Wild Carnivore Behaviour Database contains data on various aspects of carnivore ecology, including home range size, daily distance travelled, time spent active, and information in foraging niche. For the current study, I only used data from this database which were relevant to my hypotheses: chase distance (m), hunt rate (/24 hrs), kill rate (/24 hrs), and annual home range sizes (km^2).

Wild Carnivore Behaviour Database: quality inclusion checks

For inclusion into the Wild Carnivore Behaviour Database, studies had to meet the following criteria: each must be a minimum of 10 months long, thus including multiple seasons, ensuring representation of the annual ecology of the focal animals. Focal populations had to also be adult, wild, and non-provisioned, i.e. not fed by humans, nor concentrated around refuse sites.

As detailed in Section 3.2.3 I used chase distance, hunt rate, and kill rate values from the Wild Carnivore Behaviour Database to test two of my hypotheses. Note that for many species such data do not exist, resulting in relatively sparse analyses featuring these variables. For each species, I calculated the median value of each variable across all studies of that species. Additionally, for the analyses in which I added my wild foraging niche predictors to the annual home range size model (see Sections 3.1 and 3.2.5), I used median annual home range size (km^2) values extracted and calculated from this database by Miranda Bandeli.

3.2.5 Annual home range size models

As mentioned in Section 3.1 a secondary aim of this chapter is to assess whether foraging niche explains any of the variance in route-tracing *not* explained by a well-established biological risk factor it: annual home range sizes (Clubb and Mason, 2003; Clubb and Mason, 2007; Kroshko et al., 2016; with a similar trend reported in Miller, et al., 2018). I did this by comparing three model 'variants' for each wild foraging niche predictor: 1) model with just home range size as a predictor; 2) model with just the foraging niche predictor; and 3) a model with home range size and the foraging niche predictor variable.

To enable model comparison, for each model set I reduced my dataset to include species with complete data for all variables. This resulted in a loss of species especially for home range size, and thus statistical power (see Section 2.4.2), for some sets of analyses.

Therefore, if annual home range size alone (step 1) in the paragraph above) did not have approximately the expected relationship with route-tracing (i.e. a positive slope and a P value based on the t-statistic of <0.2), I did not continue with any further analyses for that set of models. Note that losing incomplete cases also resulted in sample sizes differences between my hypothesis-testing models and these ones.

I used two methods to assess whether wild foraging niche predictor variables explained the variance in route-tracing not explained by annual home range sizes: i) whether the foraging niche predictor significantly predicted route-tracing in the model including annual home range size; and/or ii) whether the model with annual home range size and the foraging niche predictor led to improvements in the former (i.e. its P value based on the t-statistic) and in model-fit overall, as judged by Adjusted R^2 values (Minitab Blog Editor, 2013).

3.2.6 Confound checks

Prior to hypothesis-testing I made two types of confound check. I checked for correlations between wild foraging niche predictors belonging to different hypotheses, using the models described in Section 3.2.7. Where correlated predictors were identified, I ran additional models during hypothesis-testing to check whether their inclusion affected interpretation of the model (in practice, they never did). Because various aspects of species life-history and biology relate to body mass (Gittleman, 1985), I also checked for relationships between body mass and my wild foraging niche predictor variables. For predictors found to significantly correlated with body mass, I controlled for body mass effects in subsequent hypothesis-testing models by including it as an extra term. I did not make such checks for prey size: predator size as body mass is an integral part of this particular variable.

Environmental conditions also affect development of stereotypic behaviours such as route-tracing and could thus potentially confound my analyses (see Section 2.4.4). Miranda Bandeli identified two aspects of species-typical husbandry that predicted route-tracing in the current dataset in re-analysis of Kroshko et al. (2016)'s data: species-typical median

degree of cover in the enclosure (ranked worst-best, 1-4) and species-typical provision of foraging enrichments (proportion of animals not given these [or if unknown whether these are provided]) (Bandeli et al., in prep). She recalculated these species-typical values from the current Captive Carnivore Database and, using these, I checked for correlations between them and my wild foraging niche predictors. Where significant relationships were identified, I controlled for these in subsequent final hypothesis-testing models by included the correlated husbandry variable as an extra term (in practice, this was never necessary).

3.2.7 Statistical analyses

All statistical analyses were performed in R (R Core Team, 2019). Models were only run if data were available for at least five species, or five species per level for categorical variables (after: Bandeli et al., in prep.). I performed phylogenetic generalised least squares (PGLS) regressions (Grafen, 1989; Pagel, 1999) in the 'caper' package (Orme, 2013) for all analyses with continuous outcomes. For binomial outcomes (here, namely hunting strategy during between-predictor checks) I used phylogenetic logistic regression models in 'phylolm' (Ho and Ané, 2014). Confound checks and most of the annual home range size models were performed over a consensus Carnivora tree from: www://10ktrees.nunn-lab.org/ (Arnold et al., 2010). Potential outliers also assessed by visually inspecting graphs and PGLS diagnostic plots (Orme, 2013). Models were compared with and without potential outliers, and if an outlier's presence did not violate the assumptions of the model, affect the overall result, and did not have a studentised phylogenetic residual >±3 (e.g. Jones and Purvis, 1997), then results were reported with the outlier. Homogeneity of residuals was checked on diagnostic plots, and normality assessed using a Shapiro-Wilk normality test, and where necessary transformations were applied to satisfy these. Pagel's Lambda (λ), a measure of phylogenetic signal (Pagel, 1999; Freckleton et al., 2002; Revell, 2010), was estimated in PGLS models using maximum likelihood. The phylogenetic logistic regression equivalent of λ is alpha (α), so this is reported in the relevant models.

To account for phylogenetic uncertainty (see Section 2.4.7), final hypothesis-testing models were performed over a tree block of 1,000 alternative Carnivora phylogenetic trees (also from: Arnold et al., 2010), as were the final models (i.e. step 3) in the annual home range size analyses (see Section 3.2.5). Model parameters from these models are summarised as medians, and their associated 95% confidence intervals are shown in square parentheses. Statistical significance was $P<0.05$, all P values are two-tailed, and results are reported to three decimal places.

3.3 Results

The species and their route-tracing and wild foraging niche predictor values are shown in Table 3.5. For 38 of the 48 species I could calculate route-tracing values for, route-tracing was the only stereotypic behaviour reported. Ten species reportedly performed other forms, but route-tracing was typically the most prevalent in these too. Within the 27 species that met the ≥5 route-tracing animals minimum inclusion criteria, grey seals, *Halichoerus grypus*, had the most time-consuming species-typical median route-tracing (53.79%), and red foxes, *Vulpes vulpes,* the least (0.16%).

Table 3.5 Carnivore comparative dataset used for all analyses. Full details of each along with their sources are described in Section 3.2.3. Variables requiring further description are as follows. Route-tracing=species-typical median % observations route-tracing. Kill rate, hunt rate, chase distance, and annual home range size were all species-typical medians. Hunting strategy is coded as pursuit (P) *versus* non-pursuit (NP). Relative prey size is the ratio between the body mass of the most common prey item a species hunts, and its own body mass. Foraging enrichment (EE)=the proportion of animals not given these (or if it is unknown if they receive them). Cover=species-typical median degree of cover within the enclosure and ranked 1-4 (worst-best).

		Outcome variable		***Species-typical wild biology predictors***								***Species-typical husbandry***	
Scientific name	**Common name**	**Route-tracing (% obs.)**	**N**	**Body mass (kg)**	**Self-hunted meat (%)**	**Kill rate (/24hr)**	**Hunt rate (/24hr)**	**Hunting strategy**	**Chase distance (m)**	**Relative prey size**	**Annual home range (km^2)**	**Foraging EE**	**Cover**
Acinonyx jubatus	Cheetah	13.55	9	50.58	100	0.85		P	240	0.67	153.86	0.43	3
Caracal caracal	Caracal	14.74	10	11.96	100			P		1.38	164.87	1	2
Catopuma temminckii	Asiatic golden cat	23.56	5	7.73	100			NP			40.15	1	2
Cryptoprocta ferox	Fossa	23	14	9.5	100			P		0.01	29.58	0.86	3
Felis margarita	Sand cat	12.68	9	2.82	100					0.03		1	3
Halichoerus grypus	Grey seal	53.79	11	197.57	100		1.7			0.01		1	
Helarctos malayanus	Malayan sun bear	18.06	26	57.08	70			NP			14.8	0.86	2
Leopardus geoffroyi	Geoffroy's cat	11.5	9		100					0.1	4.93	1	1.5
Leopardus pardalis	Ocelot	6.45	21	11.88	100			NP		0.15	10.46	0.93	2.5

		Outcome variable		***Species-typical wild biology predictors***							***Species-typical husbandry***	
Scientific name	**Common name**	**Route-tracing (% obs.)**	**N**	**Body mass (kg)**	**Self-hunted meat (%)**	**Kill rate (/24hr)**	**Hunt rate (/24hr)**	**Hunting strategy**	**Chase distance (m)**	**Relative prey size**	**Annual home range (km^2)**	**Foraging EE**	**Cover**
Leopardus tigrinus	Oncilla cat	11.5	8	2.21	100					0.08		0	2
Leptailurus serval	Serval	8.5	8	12	100		7.5	P		0	18.17	1	4
Lontra canadensis	North American river otter	5	5	8.09	100					0.01	15.71	0.67	2
Lynx canadensis	Canadian lynx	8.6	6	9.68	100	0.5		P	46	0.14	140.25	1	1.5
Lynx lynx	Eurasian lynx	10.83	10	19.3	100	0.43	1.63		20	1.04	215.65	0.33	2
Melursus ursinus	Sloth bear	15.49	5	100	70			NP			10.95	1	3
Neovison vison	American mink	8.95	7		100					0.06	0.25	0.98	2
Panthera leo	Lion	6.25	10	158.62	90	0.29	1.18	NP	26.8	0.87	214.06	0.78	3
Panthera once	Jaguar	18.69	20	83.94	100	0.17		NP	18.5	0.48	145.98	0.71	3
Panthera pardus	Leopard	9.38	35	52.4	100	0.15	1.1	NP	50.65	0.63	42.75	0.71	3
Panthera tigris	Tiger	9.43	44	161.91	100	0.14		NP	150	1.17	87.73	0.95	2
Phoca vitulina	Harbour seal	51.15	10	87.32	100		0.6			0		1	
Uncia uncia	Snow leopard	5.23	23	32.5	100	0.12		NP		1.88	68.75	0.81	3
Ursus arctos	Brown bear	19.68	44	196.29	20	0.08		NP	80		405.36	0.91	1
Ursus maritimus	Polar bear	29.78	29	371.7	100					0.27	93042.79	0.83	2
Ursus thibetanus	Asiatic black bear	7	25	99.71	20			NP			31.1	0.84	2

		Outcome variable		***Species-typical wild biology predictors***								***Species-typical husbandry***	
Scientific name	**Common name**	**Route-tracing (% obs.)**	**N**	**Body mass (kg)**	**Self-hunted meat (%)**	**Kill rate (/24hr)**	**Hunt rate (/24hr)**	**Hunting strategy**	**Chase distance (m)**	**Relative prey size**	**Annual home range (km^2)**	**Foraging EE**	**Cover**
Vulpes lagopus	Arctic fox	0.55	42	3.58	90		2.85			0.02	38.5	1	
Vulpes vulpes	Red fox	0.16	11	4.82	90	6.7	44.4	P	13.71	0.08	2.41	1	4

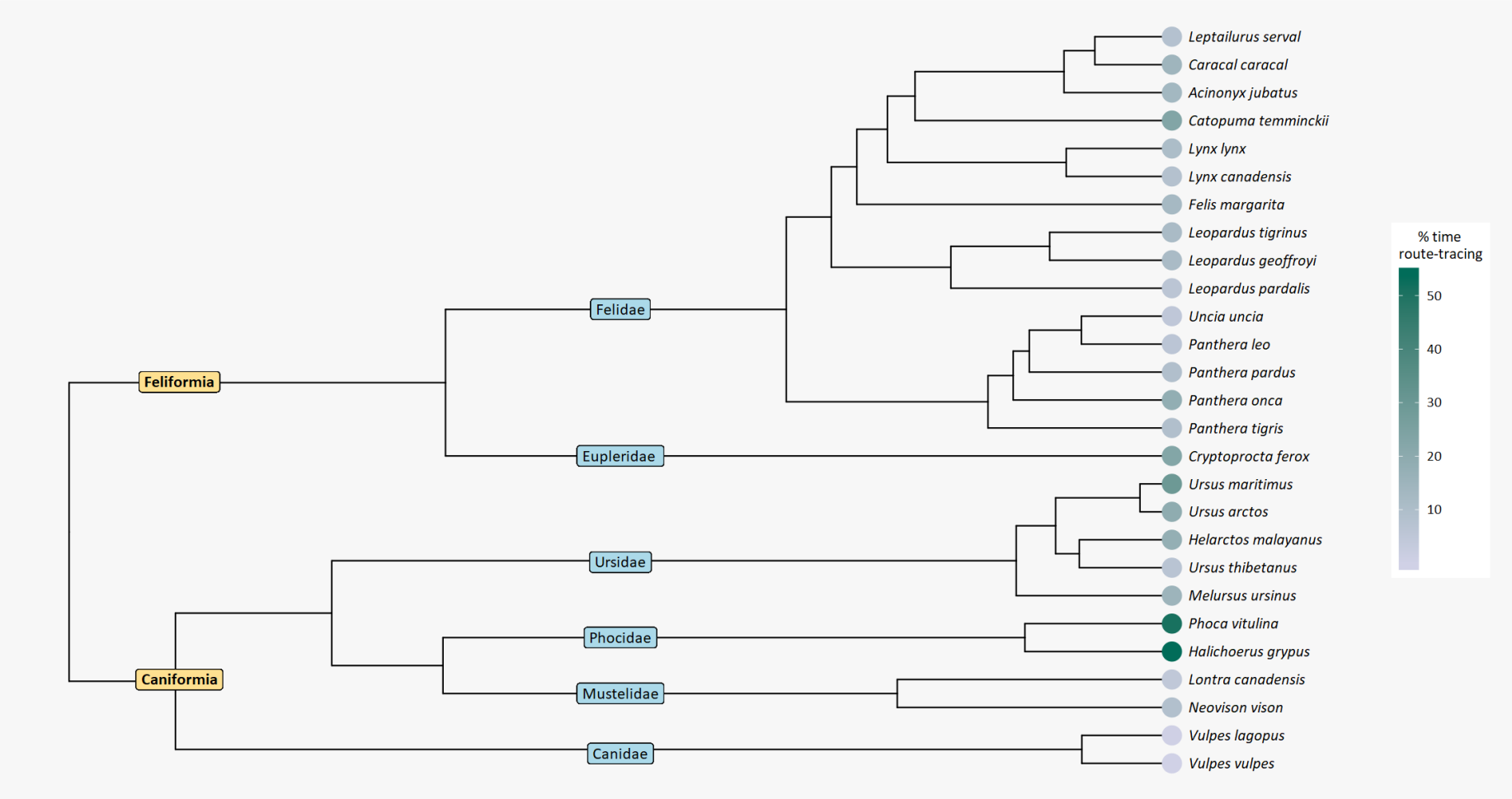

Figure 3.1 Phylogenetic tree of the 27 carnivore species featured in my analyses. Their species-typical median % observations spent route-tracing values are shown as tip points and coloured according to value (lighter colour representing less route-tracing; darker representing more). Yellow labels give suborder names, and family names are shown in blue.

3.3.1 Results of confound checks

None of my wild foraging niche predictors significantly correlated with each other (see Table 3.6), and nor did they with species-typical husbandry (see Table 3.7).

Hunt strategy and kill rate were significantly correlated with body mass: pursuit species were lighter than non-pursuit, as were species that kill the most (t_{21}=-2.664, N=23, R^2=0.253, λ=0, P=0.015; t_8 =-3.261, N=10, R^2=0.571, λ=0, P=0.012). For all hypothesis-testing models featuring these predictors, body mass was thus included.

3.3.2 Hypothesis-testing results

As shown in Table 3.8, none of my wild foraging niche predictor variables significantly predicted route-tracing. Species most reliant on self-hunted meat tended to route-trace the most (summarised results of models performed over 1,000 alternative Carnivora trees, median parameters [and their 95% confidence intervals]: t_{26}=1.871 [1.869, 1.874], N=27, R^2=0.123 [0.123, 0.123], λ=1 [1, 1], P=0.073 [0.073, 0.073]).

3.3.3 Results of annual home range size models

Results of models investigating whether any wild foraging niche predictor explains variance in route-tracing not explained by annual home range sizes (see Section 3.2.5) are shown in Table 3.9. Four of the six sets of models were fully run (because annual home range size had approximately its expected relationship with route-tracing, i.e. P<0.2 and a positive slope). Of these four, wild foraging niche predictors did not improve annual home range size's P value based on the t-statistic, nor did they improve model fit (as inferred from Adjusted R^2 values). Furthermore, the trend for species most reliant on self-hunted meat (see Section 3.3.2 and Table 3.8) disappeared once annual home range size was controlled for.

Table 3.6 Results of models investigating potential relationships between wild foraging niche predictor variables belonging to different hypotheses, and between these and annual home range sizes (a known biological risk factor for route-tracing across the Carnivora: Clubb and Mason, 2003; Clubb and Mason, 2007; Kroshko et al., 2016; with a similar trend reported in Miller, et al., 2018). To control for allometric effects (Gittleman, 1985) body mass was included as a term in all models featuring annual home range size. PGLS models were used for continuous outcomes, and phylogenetic logistic regression was used to analyse hunting strategy as an outcome. Dashes indicate too few species were available for analysis (fewer than five species for continuous predictors, or fewer than five species per level for categorial predictors). Results were considered significant at P<0.05, and trends (P<0.10) are italicised. All P values are two-tailed.

Hypothesis:	*i. route-tracing is redirected hunting*			*ii. restricting pursuit hunters leads to route-tracing*		*iii. restricting hunting of relatively large prey items*	
Outcome: **Predictor:**	**Reliance on self-hunted meat (%)**	**Hunt rate (/24hr)**	**Kill rate (/24hr)**	**Hunting strategy (pursuit v non-pursuit)**	**Chase distance (m)**	**Relative prey size**	**Annual home range size (km^2)**
Reliance on self-hunted meat (%)				$Z=1.419$, $N=17$, $\alpha=0.012$, $P=0.156$	$t_7=0.061$, $N=9$, $R^2=0.001$, $\lambda=0$, $P=0.953$	$t_{20}=-0.406$, $N=22$, $R^2=0.008$, $\lambda=0.603$, $P=0.689$	$t_{18}=1.702$, $N=21$, $R^2=0.419$, $\lambda=0$, $P=0.106$
Hunt rate (/24hr)				-	-	$t_6=-0.241$, $N=8$, $R^2=0.010$, $\lambda=0.285$, $P=0.818$	$t_3=-0.688$, $N=6$, $R^2=0.473$, $\lambda=0$, $P=0.541$

Hypothesis:	*i. route-tracing is redirected hunting*			*ii. restricting pursuit hunters leads to route-tracing*		*iii. restricting hunting of relatively large prey items*	
Outcome: **Predictor:**	**Reliance on self-hunted meat (%)**	**Hunt rate (/24hr)**	**Kill rate (/24hr)**	**Hunting strategy (pursuit v non-pursuit)**	**Chase distance (m)**	**Relative prey size**	**Annual home range size (km²)**
Kill rate (/24hr)				-	t_7=-0.203, N=9, R^2=0.006, λ=0, P=0.845	*t_7=-2.172, N=8, R^2=0.403, λ=0, P=0.066*	t_7=0.191, N=10, R^2=0.424, λ=1, P=0.854
Hunting strategy (pursuit v non-pursuit)	t_{15}=0.620, N=17, R^2=0.025, λ=0.736, P=0.544	-	-			t_{10}=-1.449, N=12, R^2=0.173, λ=0, P=0.178	t_{14}=-1.394, N=17, R^2=0.379, λ=0.359, P=0.185
Chase distance (m)	t_7=0.179, N=9, R^2=0.005, λ=1, P=0.179	-	t_7=-0.269, N=9, R^2=0.010, λ=1, P=0.795			t_6=1.077, N=8, R^2=0.162, λ=0, P=0.323	t_6=-1.731, N=9, R^2=0.531, λ=0.999, P=0.134

Hypothesis:	*i. route-tracing is redirected hunting*			*ii. restricting pursuit hunters leads to route-tracing*		*iii. restricting hunting of relatively large prey items*	
Outcome: **Predictor:**	**Reliance on self-hunted meat (%)**	**Hunt rate (/24hr)**	**Kill rate (/24hr)**	**Hunting strategy (pursuit v non-pursuit)**	**Chase distance (m)**	**Relative prey size**	**Annual home range size (km²)**
Relative prey size	t_{20}=-0.407, N=22, R^2=0.008, λ=0.602, P=0.689[a]	t_7=0.179, N=9, R^2=0.005, λ=1, P=0.179	t_7=-1.468, N=9, R^2=0.236, λ=1, P=0.185	Z=-0.0011, N=12, α=0.040, P=0.999	t_6=0.797, N=8, R^2=0.096, λ=0, P=0.456		t_{13}=1.104, N=16, R^2=0.346, λ=1, P=0.290
Annual home range size (km²)	*t_{18}=1.881, N=21, R^2=0.208, λ=0.363, P=0.076*	*t_3=-2.406, N=6, R^2=0.745, λ=0, P=0.095*	t_7=-1.253, N=10, R^2=0.649, λ=0, P=0.251	Z=0.920, N=17, α=0.131, P=0.358	t_6=-0.226, N=9, R^2=0.045, λ=0, P=0.829	t_{13}=-0.202, N=16, R^2=0.339, λ=0, P=0.843	

[a]note that residuals from this model did not pass a Shapiro-Wilk normality test (various transformations were applied but did not help achieve normality). Therefore, this result should be treated with caution.

Table 3.7 Results from PGLS models assessing relationships between wild foraging niche predictor variables and two aspects of species-typical husbandry (see Section 3.2.6. Dashes indicate that fewer than five species had data for both variables, and so the model was not performed (see Section 3.2.5). Species-typical median degree of cover was ranked worst to best (1-4). Species-typical foraging enrichment provision was the proportion of animals not given these (or if unknown whether these are provided). Results were significant at P<0.05, and trends (P<0.10) are italicised.

Wild foraging niche predictor	Species-typical degree of cover	Species-typical foraging enrichment provision
Reliance on self-hunted meat (%)	t_{22}=1.527, N=24, R^2=0.096, λ=0, P=0.141	t_{25}=-0.527, N=27, R^2=0.011, λ=0, P=0.603
Hunt rate (/24hr)	-	t_6=0.813, N=8, R^2=0.100, λ=0.155, P=0.447
Kill rate (/24hr)	t_8 =1.280, N=10, R^2=0.170, λ=0.920, P=0.236	t_8 =1.669, N=10, R^2=0.258, λ=0, P=0.134
Hunting strategy (pursuit v non-pursuit)	t_{15}=1.249, N=17, R^2=0.094, λ=0, P=0.231	*t_{14}=2.085, N=16, R^2=0.237, λ=0, P=0.056*[a]
Chase distance (m)	t_7=-1.190, N=9, R^2=0.168, λ=1, P=0.273	t_7=-0.638, N=9, R^2=0.055, λ=0, P=0.544
Relative prey size	t_{17}=-0.172, N=19, R^2=0.002, λ=0, P=0.866	t_{20}=-1.311, N=22, R^2=0.079, λ=0, P=0.205

[a] outlier removed: cheetah

Table 3.8 PGLS results of final hypothesis-testing models performed over a tree block of 1,000 alternative Carnivora phylogenetic trees. Here, results of these models are summarised to the median value for each parameter and its 95% confidence intervals (shown in square parentheses). Results were considered significant at P<0.05, and trends (P<0.10) are italicised. All P values are two-tailed.

Predictor variables	Results
Hypothesis i: route-tracing is re-directed hunting:	
Reliance on self-hunted meat	*t_{25}=1.871 [1.869, 1.874], N=27, R^2=0.123 [0.123, 0.123], λ=1 [1, 1], P=0.073 [0.073, 0.073]*
Hunt rate (/24hrs)	t_7=-0.524 [-0.525, -0.523], N=9, R^2=0.044 [0.044, 0.044], λ=1 [1, 1], P=0.619 [0.618, 0.620]
Kill rate (/24 hrs)*	t_7=-1.514 [-1.514, -1.514], N=10, R^2 =0.410 [0.410, 0.410], λ<0.001 [<0.001, <0.001], P=0.174 [0.174, 0.174]
Hypothesis ii: restricting pursuit hunters leads to route-tracing	
Hunting strategy (pursuit v non-pursuit)*	t_{14}=-0.184 [-0.184, -0.184], N=17, R^2 =0.009 [0.009, 0.009], λ<0.001 [<0.001, <0.001], P=0.856 [0.856, 0.856]
Chase distance (m)	t_7=0.166 [0.165, 0.167], N=9, R^2 =0.004 [0.004, 0.004], λ=1 [1, 1], P=0.873 [0.872, 0.874]
Hypothesis iii: restricting the hunting of relatively large prey items leads to route-tracing	
Relative prey size	t_{20}=-0.053 [-0.048, 0.060], N=22, R^2<0.001 (<0.001, <0.001), λ=1[1, 1], P=0.952 [0.947, 0.956]

***** Body mass included in all models, see Section 3.2.6 for justification.

Table 3.9 PGLS models investigating whether adding any of my wild foraging niche predictor variables explains the variance in route-tracing not explained by annual home range sizes (a known biological risk factor for route-tracing across the Carnivora: Clubb and Mason, 2003; Clubb and Mason, 2007; Kroshko et al., 2016; with a similar trend reported in Miller, et al., 2018). In all cases species-typical median % observations route-tracing was the outcome. Body mass was included in all models featuring annual home range size to control for allometric effects (Gittleman, 1985). Results given under 'Model 1' refer to a model with annual home range size only; 'Model 2' refers to a model with the focal wild foraging niche predictor only. 'Model 3' refers to results of a model featuring annual home range size and the focal wild foraging niche predictor, performed over a tree block of 1,000 alternative Carnivora trees (these results are summarised as medians and corresponding 95% confidence intervals in square parentheses). Dashes indicate that annual home range size's usual relationship (see Section 3.2.5) with route-tracing did not emerge in Model 1. I assessed the effect adding wild foraging niche predictor by visually comparing Model 1 and 3s' Adjusted (Adj.) R^2, and annual home range size's P value based on the t-statistic values, i.e. larger Adj. R^2 and smaller P values would indicate improvements. Results were considered significant at P<0.05 and shown in bold, trends (P<0.10) are italicised. All P values are two-tailed.

Predictors	Model 1	Model 2	Model 3: individual term parameters	Model 3: whole model parameters	Comments
Annual home range size (km^2)	**t_{18}=2.336, N=21, Adj. R^2=0.195, λ=0.588, P=0.031**		t=1.660 [1.659, 1.660], P=0.115 [0.115, 0.115]	$F_{3, 17}$=2.700 [2.697, 2.703], N=21, Adj. R^2=0.203 [0.203, 0.204], λ=0.772 [0.772, 0.773]	No improvement, and the previous trend for reliance on self-hunted meat to predict route-tracing disappears once annual home range size is controlled for
Reliance on self-hunted meat (%)		t_{19}=1.680, N=21, Adj. R^2=0.084, λ=1, P=0.109	t=1.031 [1.030, 1.032], P=0.317 [0.316, 0.318]		

Predictors	**Model 1**	**Model 2**	**Model 3: individual term parameters**	**Model 3: whole model parameters**	**Comments**
Annual home range size (km^2) Hunt rate (/24hrs)	t_3=0.497, N=5, Adj. R^2=-0.429, λ=1, P=0.654	-	-		Did not pass step 1
Annual home range size (km^2) Kill rate (/24hrs)*	t_7=1.885, N=10, Adj. R^2=0.332, λ=0, P=0.101	t_7=-1.515, N=10, Adj. R^2=0.241, λ=0, P=0.174	t=1.540 [1.540, [1.540], P=0.174 [0.174, 0.174] t=-1.172 [-1.172, -1.172], P=0.286 [0.286, 0.286]	$F_{3, 6}$=2.727 [2.727, 2.727], N=10, Adj. R^2=0.365 [0.365, 0.365], λ<0.001 [<0.001, <0.001]	No improvement
Annual home range size (km^2) Hunting strategy (pursuit v non-pursuit)*	t_{14}=1.149, N=17, Adj. R^2=-0.038, λ=0, P=0.270	-	-		Did not pass step 1

Predictors	**Model 1**	**Model 2**	**Model 3: individual term parameters**	**Model 3: whole model parameters**	**Comments**
Annual home range size (km^2)	t_6=1.711, N=9, Adj. R^2=0.420, λ=0, P=0.138		t=1.561 [1.561, 1.561], P=0.179 [0.179, 0.179]	$F_{3, 5}$=3.676 [3.673, 3.679], N= 9, Adj. R^2=0.308 [0.308, 0.308], λ<0.001 [<0.001, <0.001]	No improvement
Chase distance (m)		t_7=0.164, N=9, Adj. R^2=-0.139, λ=1, P=0.874	t=0.176 [0.176, 0.176], P=0.867 [0.867, 0.867]		
Annual home range size (km^2)	*t_{13}=2.139, N=16, Adj. R^2=0.314, λ=0.692, P=0.052*		*t=2.152 [2.151, 2.152], P=0.052 [0.052, 0.053]*	$F_{3, 12}$=2.882 [2.880, 2.884], N=16, Adj. R^2=0.273 [0.273, 0.274], λ=0.811 [0.811, 0.812]	No improvement
Relative prey size		t_{14}=-0.326, N=16, Adj. R^2=-0.063, λ=0.911, P=0.750	t=-1.022 [-1.023, -1.020], P=0.327 [0.327, 0.328]		

*body mass included in all models (see Section 3.2.6)

3.4 Discussion

In this chapter my results do not support my hypotheses that (i) route-tracing represents redirected hunting, or that either (ii) restricting pursuit hunters or (iii) restricting hunting of relatively large prey items lead to route-tracing. Regarding the secondary aim of this chapter, I also did not find any evidence that foraging niche explains variance in route-tracing not explained by annual home range sizes. Furthermore, the one trend that did emerge between reliance on self-hunted meat (used to infer motivation to hunt) and route-tracing, disappeared once annual home range size was controlled for.

Limitations to this study might include data quality. The minimum inclusion criteria for studies entered into the Captive Carnivore Database was 1 day: necessary because this type of study is typically short, but likely introduces noise into the dataset and limits representativeness. Reports of animals' rearing and living conditions varied from being extensive to non-existent, which may hamper the effectiveness of my species-typical husbandry variables as statistical controls. Only ~10% (27) of the >250 Carnivora species (cf. Wozencraft, 2005) were included in my dataset, which may restrict generalisability of my findings across the entire group. Reflective of research bias in the literature, some groups such as the Pantherinae were well-sampled (I had route-tracing data for five of the seven species within this subfamily), whereas others like the Mephitidae were not sampled at all. Lack of generalisability is further exacerbated by the few available wild foraging niche data for some analyses. My sparsest hypothesis-testing models, chase distance and kill rate (see Table 3.8) featured just nine species with a bias towards Pantherinae. Blomberg et al. (2003) argue a minimum sample size of 20 species is required during comparative analyses, for acceptable power and Type I error rates (an issue I return to below). Therefore, my models with fewer species than this are likely underpowered, prone to Type I and II error, and more strongly affected by other issues such as leverage (e.g. Mundry, 2014). Nevertheless, results of my two better-sampled hypothesis-testing models, reliance on self-hunted meat and relative prey size, also ultimately led to rejection of their respective hypotheses (the trend associated with the former disappeared one annual home range size was controlled for, see Table 3.9). Therefore, when my results are considered alongside the points I make next, it

seems the overall evidence most likely supports that route-tracing does *not* relate to hunting.

Firstly, if route-tracing does not relate to hunting, then why does is have the relationship it usually does with feeding times (i.e. most intensive before feeding and usually ceasing afterwards: Mason, 1993; Weller and Bennett, 2001; Vickery and Mason, 2004)? Anticipation might explain this (sensu Watters, 2014). Some authors have hypothesised that stereotypic behaviours, such as route-tracing, can become emancipated and elicited by stimuli aside from its original (Lawrence and Terlouw, 1993; Mills and Luescher, 2006), such as anticipation of being fed. As with most zoo animals (Waitt and Buchanan-Smith, 2001) of the captive individuals with feeding regime information in my dataset, I note anecdotally that they were usually fed at regular, predictable times each day. Cues associated with food delivery, e.g. the sounds, sights and smell of food being prepared, are also easily learnt and trigger can route-tracing (Mason, 1993; Carlstead, 1998; Vickery and Mason, 2004). Therefore, most of the animals in my dataset could likely predict and anticipate food arrival. For the route-tracers this could elicit route-tracing, with the very arrival of food potentially reinforcing the behaviour.

Secondly, why is route-tracing more prevalent in Carnivora than other mammalian orders (Mason et al., 2007)? While diet, and implicitly hunting, appears the obvious explanation, ranging might better explain this prevalence-bias. As already discussed, large annual home range size is a known biological risk factor for route-tracing (Clubb and Mason 2003, 2007; Kroshko et al., 2016; with a similar trend in: Miller et al., 2018). Carnivorous species have larger home range sizes than omnivores and herbivores (Harestad and Bunnel, 1979), and many species within Carnivora are carnivorous. For example, of 230 Carnivora species categorised, 47% were carnivorous whereas just 3% were herbivorous, but of 229 Ungulata species 21% were carnivorous and 66% herbivorous (Jones et al., 2009). Following this logic, the higher prevalence of route-tracing within Carnivora could simply reflect the order's relatively larger home range sizes. A similar relationship between ranging behaviour, namely daily travel distances, and route-tracing is also found in Primates (Pomerantz et al., 2013).

Thus, a testable hypothesis is that that ranging could be a risk factor for route-tracing across taxa (see also Table 2.1).

Thirdly why, given my results, did chase distance emerge as a risk factor for route-tracing in Kroshko et al. (2016)'s study? Differences in software (phylogenetically independent contrasts *versus* PGLS) and phylogenetic tree used (Nyakatura and Bininda-Emonds, 2012 *versus* Arnold et al., 2010) do not explain this: I replicated Kroshko et al. (2016)'s significant result using their data with PGLS and the consensus tree I used throughout this chapter (result not shown). Neither do differences in species included in the analysis, as when I used my updated values for the five species in Kroshko et al. (2016)'s chase distance analysis, the model was non-significant (result not shown). While my chase distance hypothesis-testing model had few species (eight), Kroshko et al. (2016)'s was even sparser, with just five (far fewer than the recommended N≥20: Blomberg et al., 2003). Therefore, the most likely explanation is Kroshko et al. (2016)'s result was Type I error, highlighting how important an adequate sample size (N of species) is for comparative analyses: an issue also potentially relevant in my study.

No aspect of foraging niche was found to explain any of the route-tracing variance not explained by annual home range size (Table 3.9). This further emphasises that the evolutionary basis for this form of stereotypic behaviour relates to ranging rather than hunting. Therefore, despite hunting seeming so critical to wild survival and that it persists regardless of failures and costs (e.g. Smith, 1980; Holekamp et al., 1997; Carbone et al., 2007; Caro, 2017), perhaps the lack of relationship between hunting and route-tracing found here should not be surprising. Many wild carnivores are widely reported to consume meat not killed themselves, whether scavenged or kleptoparastised (Curio, 1976; Iyengar, 2008; Knopff et al., 2010; Jacobson et al., 2016). So, the option of consuming 'free' food seems a good option for captive hunters too.

3.4.1 Recommendation for zoos and future research

An important benefit of a phylogenetic comparative welfare study is that results aid targeted practical recommendations to improve welfare in affected species, along with fundamental, long-term collection planning benefits (as advocated in Chapter 2). As no foraging niche predictor emerged as a risk factor for route-tracing, I am unable to make such recommendations. However, continued investment in foraging enrichments should not cease just because foraging niche did not predict route-tracing. Animals readily use and value foraging enrichments, and they often improve welfare (e.g. Markowitz and LaForse, 1987; Forthman et al., 1992; Shepherdson et al., 1993). Rather, attention should be shifted towards understanding which aspects of carnivore biology *do* relate to route-tracing. Currently, work is ongoing to better understand which aspects of ranging explains route-tracing across the Carnivora, e.g. novelty associated with a nomadic lifestyle, or ranging behaviour flexibility (Bandeli et al., in prep.).

The Captive Carnivore Database is useful in highlighting specific species and groups requiring attention. As already mentioned, some families are entirely missing (Mephitidae, Nandiniidae, and Herpestidae), meaning the route-tracing status of these species is unknown, and worthy of investigation. One notable species stood out from others for a different reason. Pallas' cat featured in the database and was well-sampled enough (N=8) for potential inclusion in analyses, but was excluded because none reportedly route-traced (note that no black-footed cats, *Felis nigripes*, or cape fur seals, *Arctocephalus pusillus*, route-traced either, but each of these species were represented by just two animals [see Appendix 3]). Pallas' cats might be innately predisposed to good captive welfare, hence no route-tracing. However, they have a relatively large home range size for their body size (89.5 km^2; 3.05 kg), making this seem unlikely. Perhaps these cats are simply performing abnormal behaviours outside of typical zoo study observation times (i.e. opening times; an issue that may be relevant throughout my dataset). Or, instead, a very specific form of inactivity indicative of a depression-like state may be an alternative behaviour to route-tracing (in mice, *Mus musculus*: Fureix et al., 2016). Potentially then, as emphasised elsewhere some species might be more inclined towards this contrasting indicator of

compromised welfare. Inspired directly by the unusual lack of route-tracing by the Pallas' cats in this study, work is now underway to establish the captive welfare status, and other management problems of this species (Díez-León et al., in prep.). Contrastingly, other species are noted for the severity of their route-tracing, and efforts should be focussed on addressing this welfare problem of these species (e.g. by incorporating practical recommendations made in: Bandeli et al., in prep.; or by choosing to keep less prone species). Grey seals and harbour seals had the most time-consuming route-tracing of all (53.79 and 51.15%, respectively) and walrus the third (51.27%; see Appendix 3, as this value corresponds to four animals, thus excluding it from analyses). Although not as severe as the seals, the polar bear is another marine species with relatively high levels of route-tracing (29.78%). So, is there something unique to marine species which explains the high levels of route-tracing by these species? If so, I would predict that other seals and marine species would perform similar levels of route-tracing too. Alternatively, because the two seals lacked annual home range size values, this apparent pattern might instead reflect the annual home range size effect. In which case, based on their typical time devoted to route-tracing, one would predict that these species also have relatively large annual home range sizes – and this could be confirmed in the field.

As described in my limitations paragraph (Section 3.4), the quality of the data held within the Captive Carnivore Database is entirely reflective of the published works it is built upon. This meta-analytical approach comes with many benefits: it is non-invasive and does not directly comprise animal welfare; it is cheap to run in terms of finances and time; and as it may include data from animals in collections worldwide, it has potential to be valuably generalisable across a population, unlike the more typical single-species, often single-zoo study (see also Section 2.4.3.3). However, this approach comes with the following limitations. Across published zoo literature, information on rearing history and current living conditions of focal animals is patchy, as reporting varied wildly between studies. This affects how well one can control for these effects (important because they *also* can affect welfare-relevant outcomes; see Section 2.4.4). Reporting of behaviour, including stereotypic behaviour, also varies from study to study. To illustrate, for route-tracing some studies provided mean values per individual; others reported one mean across all route-tracing

individuals; and yet others reported a mean value across *all* individuals, including non-route-tracers, rendering those values useless for our purposes. Regarding the latter emphasises another point: our focus here had to be on route-tracers only, because research bias towards stereotypic animals prevents accurate calculation of population-level estimates of severity and prevalence (see also Section 2.4.3.3). This is not a minor issue, as it limits our understanding of the full extent of route-tracing. As already acknowledged, including studies that are only a minimum of 1 day long restricts the representativeness of the behaviour recorded. Necessity dictates that many zoo observational studies are short in timeframe, e.g. because of staff time commitments and/or being student projects. Such studies also often have small sample sizes, and if focal animals are from the same zoo, possibly also sharing an enclosure, then this brings with it issues around (non)independence of datapoints (e.g. Crockett and Ha, 2010). Nevertheless, meta-analytical techniques, such as used here, can make good use of small studies by effectively pooling them, this increasingly power and generalisability (Nakagawa and Santos, 2012; Meta-analysis in Basic Biology, 2016). However, when such studies are also affected by the other problems just described, between-study variation combined with short, possibly non-representative and -independent values for behaviour limits the fundamental value of such zoo observational studies. Luckily, these problems are easily addressed by the implementations I discuss next.

Firstly, to better enable meta-analytical methods and generally improve quality, I would encourage standardisation of reporting appropriate to the taxonomic group (here, what I describe is appropriate for Carnivora, but would likely need tailoring for other taxa, e.g. those living in large groups and/or difficult to individually identify). For instance, as typical for field studies of wild animal behaviour, descriptive statistics of broad behavioural categories should be included in results to enable proper comparability between studies. This might include means and standard errors of % time spent foraging, travelling, resting, and socialising, with the addition of time devoted to stereotypic behaviours, if any (these being validated welfare indicators of captive animals [see Section 1.2.2] and thus an important behavioural category). Ideally, these descriptive statistics should be reported at the individual-level: achievable for most Carnivora species with adequate familiarisation of focal animals. Additionally, at minimum I would also recommend reporting origin, rearing

history and living conditions (e.g. enclosure size, group size, furniture, diet, and enrichment routine) of all focal animals. As already emphasised, these measures can also affect outcome variables (see Section 2.4.4) and providing this key information would enable better statistical control for their effects during analyses. Animal identifiers such as Species360 identification numbers and/or international studbook numbers should also be provided, as this would enable the tracking of an animal's behaviour across studies longitudinally – a fascinating avenue of research. While some may prefer anonymity, identification of zoos within studies would also be beneficial (especially from a statistical viewpoint) and would also help zoos visibly meet their research obligations (Hosey et al., 2013d). Finally, there is also another type of generalisability to address. I would encourage zoos and their researchers to actively address the research bias, and 'fill in the gaps' by taking species noted by their absence in the zoo literature and, subsequently, the current Captive Carnivore Database into the collective research effort.

Naturally, introducing these sorts of standards requires input from interested parties. Therefore, conversation is needed between zoo researchers, relevant Taxon Advisory and Working Groups, and students and their supervisors to decide appropriate standards to set and ensure the success of changes made is adequately reviewed and amended as required. Importantly though, the suggestions I make above are easily implemented without impinging on researchers' autonomy and intellectual freedom in addressing their specific research questions. Standardisation of reporting would improve the quality and validity of published zoo observational studies, even those very short in time; better facilitate future meta-analytical studies like the current one, with all the welfare and collection management benefits they can provide (see Chapter 2 and advocated by: Dawkins, 2006); may provide opportunity to use even more sophisticated statistical approaches (such as phylogenetic generalised linear mixed models whose use was precluded here because of limitations already discussed; see Appendix 1); improve generalisability, and permit calculation of population-level indices of welfare-relevant outcomes; and, ultimately, have potential to effectively and efficiently improve wellbeing for many thousands of animals. With a pool of thousands of students and other researchers on a yearly basis wishing to measure the behaviour of zoo animals and hoping to publish their work, the zoo community is an

enviable position with potential to better understand, and thus improve, the welfare of its animals.

3.5 Conclusions

Despite some indirect support that restricting hunting in captive carnivores leads to route-tracing, I found no aspect of wild foraging niche to predict route-tracing. Thus, I found no support that route-tracing represents re-directed hunting; that it relates to restriction of pursuit-style hunting; nor that it relates to restricting the hunting of relatively large prey items. Furthermore, none of my wild foraging niche predictor variables explained any of the variance in route-tracing not explained by a known biological risk factor for it: annual home range sizes. Between-order differences in typical annual home range sizes, which is affected in part by diet, could help explain the Carnivora-bias in route-tracing. The usual pre-feeding peak in route-tracing of captive carnivores might result from stereotypic behaviour being elicited by stimuli, namely feeding anticipation, aside from the original trigger. Finally, my results suggest that a previous comparative study's finding that wild chase distances predicts route-tracing severity, is likely Type I error associated with a small sample size. Whilst my results prevent me from making targeted recommendations to improve welfare, they do valuably yield areas for future research. There are now several specific species and families requiring research attention to better understand their welfare, either because they are missing in the literature due to research bias, or because their typical route-tracing is so severe. Finally, I propose that easily implemented standardisation of reporting of behaviour, rearing history and living conditions within published studies of captive animals would improve the scientific value of zoo-based studies; better facilitate meta-analytical, cross-species studies such as this one; and, ultimately, improve welfare across this charismatic taxonomic group and others.

Chapter 4: Feather-damaging pet parrots: what is the influence of wild foraging behaviour?

Abstract

Feather damaging behaviour (FDB) is a self-directed behaviour performed by some captive parrots wherein the bird chews and/or plucks feathers, and it is a welfare problem. Different biological risk factors have been previously identified for FDB and other stereotypic behaviours (SB; whole-body and other oral forms). Thus, based on two aspects of natural foraging (food-search and -handling) relatively long 'food search times' predicted FDB, whereas relatively large brain volumes predicted whole-body and oral SBs. My primary aim here was to unpick FDB's risk factor, thus informing the best way to address it. Based on supporting evidence I hypothesised that FDB relates specifically to food handling times; re-examined whether oral SBs also relate to food handling; and tested if restricting ranging associated with wild food search predicts route-tracing. For my second aim, I assessed inter-relationships among whole-body SBs (route-tracing, spinning, stationary whole-body, and head-only SBs), oral SBs, and FDB to inform the most appropriate method of analysing these behaviours. Subsequently, I assessed whether wild foraging behaviour explained variance in other SBs not explained by relative brain volumes. Species-typical prevalence of FDB, other SBs and of corresponding husbandry conditions were calculated from survey responses regarding 1,378 parrots from 50 species. From published literature I calculated two wild foraging behaviour predictors: species-typical relative reliance on food requiring i) long search, and ii) extensive oral manipulation (i.e. food handling). Using phylogenetic generalised least squares regressions to control for non-independence of species datapoints, I found species reliant on wild food requiring extensive oral manipulation to have more prevalent FDB. Regarding my secondary aim, all five subtypes of other SBs

significantly positively correlated with at least one other, but their relationships with FDB were weaker. Given the subtypes of other SBs share a biological risk factor – large relative brain volumes – for analyses pooling them into a single 'all other SB' outcome measure is appropriate. Neither wild foraging behaviour predictor explained any variance in other SBs not explained by relative brain volumes. Overall, my results indicate FDB and other SBs are distinct forms of abnormal behaviour, and that the latter may be different responses to the same captive challenge (i.e. being relatively large-brained). Based on identification of FDB's risk factor, I make practical recommendations to help address FDB; suggest species predisposed to being less suitable for the pet trade; and detail species needing research attention, as their populations have such prevalent behavioural problems. Should these issues prove difficult to resolve, their continued use in the pet trade must be questioned.

4.1 Introduction

Feather damaging behaviour (FDB) is a typically self-directed abnormal repetitive behaviour performed by some captive parrots (see Figure 4.1), in which the bird chews and/or plucks feathers (Meehan et al., 2003b; van Zeeland et al., 2009). Around 10-15% of pet parrots are affected by FDB and its effects (Grindlinger and Ramsay, 1991; Gaskins and Bergman, 2011; McDonald Kinkaid et al., 2013), which include blood loss and infection, hypothermia (Meehan et al., 2003b; van Zeeland et al., 2009), and increased likelihood of relinquishment to rehoming centres (Meehan, 2003; Gaskins and Bergman, 2011). FDB is a multifactorial welfare-relevant management problem, being comorbid with certain infections (e.g. ectoparasites: Doneley, 2009) and disease (e.g. renal disease: Burgos-Rodríguez, 2010); with demographic (e.g. being female: McDonald Kinkaid et al., 2013), environmental (e.g. social isolation: Meehan et al., 2003a) and biological risk factors (reviewed by van Zeeland et al., 2009; Mellor et al., 2018a), the latter being the main focus of this chapter.

Figure 4.1 An African grey parrot, *Psittacus erithacus*, with feather-damaging behaviour.

Photo credit: Yvonne van Zeeland

Wild parrots spend 40-75% of their active time foraging (Magrath and Lill, 1983; Westcott and Cockburn, 1988; Renton, 2001), in contrast to captive parrots, e.g. ~6% of active time for captive orange-winged Amazon parrots, *Amazona amazonica*, on a regular pelleted diet (Rozek et al., 2010). This mismatch has been widely hypothesised to result in the expression of abnormal oral behaviours in birds (Keiper, 1969; Meehan et al., 2004), including FDB in parrots (Meehan et al., 2003b; van Zeeland et al., 2009). Thus, along with other potential biological risk factors for poor psittacine welfare, wild foraging behaviour was examined in a previous comparative study (McDonald Kinkaid, 2015). McDonald Kinkaid (2015) reported that species with naturally long 'relative food search times' have more prevalent FDB in captivity, whereas a proxy for intelligence, relative brain volume, predicted other forms of stereotypic behaviours (SBs) – repetitive behaviours reflecting poor welfare (see also Section 1.2.2; Mason, 2006b) – including other forms of oral abnormal behaviours (a result I recently confirmed and replicated using more up-to-date phylogenetic information and software: McDonald Kinkaid et al., in prep.). Note that while feather-damaging behaviour is *also* a stereotypic behaviour (sensu Mason, 2006b), for simplicity here I use the term 'other SBs' to mean abnormal repetitive behaviours *excluding* FDB. Through necessity, as data on foraging behaviour of wild parrots were scarce at the time of writing, McDonald Kinkaid (2015)'s 'relative food search times' variable was a broad categorical predictor: 'long' *versus* 'short'. She attributed species to one of these categories based on two characteristics of the predominant food type in the species-typical wild diet: i) its accessibility, and ii) its discoverability. Species were assigned to the 'long' food search times category if their main food is relatively time-consuming to access, requires quality assessment and/or physical manipulation (i); or if it is time-consuming to find, i.e. scarce, inconspicuous, and/or patchily-distributed in space and time (ii). Conversely, if the main food type is relatively quick to access, requires no/little assessment or manipulation (i), and is quick to find as abundant, conspicuous and/or evenly-distributed (ii), then the species was attributed to the 'short' category.

'Relative food search times', however, pools two distinct aspects of appetitive foraging behaviour involving different mechanisms (sensu Rowland and Mathes, 2008). The first phase describes behaviours that bring an animal into contact with food (i.e. locomotor

search), while behaviours belonging to the second are those triggered by the food item's feel and taste (i.e. food handling, which for parrots is typically oral), ultimately resulting in a decision whether to swallow or eject it (Rowland and Mathes, 2008). Recommendations based on identification of biological risk factors are made according to the nature of the risk factor itself (see Chapter 2). For this reason, pooling of distinct aspects of behaviour may limit the quality of such recommendations. For instance, if FDB is predicted by diets associated with long search time, e.g. extensive travel between patches, then different recommendations would be made than if, instead, it were predicted by diets requiring long food handling times, i.e. extensive oral manipulation to access. To address problems effectively via the targeted recommendations this research approach can generate (see Chapter 2), it is essential to be precise. Therefore, further examination of the role natural foraging behaviour has on FDB is now required, by unpicking McDonald Kinkaid (2015)'s 'relative food search times' risk factor.

Considering the wild food-search and -handling behaviours of parrots, there are potential welfare-relevant mismatches in each case. Captivity's inherent spatial restrictions physically prevent travel of any great distance, thus limiting searching behaviour; and structural differences between wild and captive diets might create a mismatch in food handling times. Regarding FDB, it is the latter I focus on here as being the most biologically relevant predictor of FDB for the following reasons. Pelleted diets are usually recommended for captive psittacines, being considered nutritionally complete (Ullrey et al., 1991; Koutsos et al., 2001), but these require very little manipulation and are thus quick to consume (Oviatt and Millam, 1997; Meehan et al., 2003b). This contrasts with the handling time required to access some wild food items. For instance, parrots usually remove seed husks before eating the kernel (Ullrey et al., 1991; Koutsos et al., 2001), and harder nuts and seeds especially likely require extensive oral manipulation by the bird (e.g. great green macaws, *Ara ambigua*, eat "very hard-shelled" *Lecythis costaricensis*: del Hoyo et al., 1997). Some species show physical adaptations for handling very hard food items, e.g. they possess a suborbital arch and its associated muscle (*musculus pseudomasseter*), which confer increased crushing power and dexterity (Homberger, 2006; Toft, 2015). Buried insects and their larvae also require oral manipulation, i.e. digging, and the bills of species reliant on these sources have

elongated and pick-like upper mandibles to facilitate this (Cameron, 2012). That captive parrots freely participate in extra foraging opportunities made experimentally available, would imply standard pelleted diets may indeed not meet the behavioural needs of the birds (Rozek and Millam, 2011). Rozek and Millam (2011) found that orange-winged Amazon parrots were strongly motivated to access over-sized pellets (~20-30 times larger than regular-sized pellets), and their foraging times increased from 5.9% when fed regular-sized pellets to 25.7% of active time when fed over-sized pellets (Rozek et al., 2010). If some species are motivated to perform extensive oral manipulatory behaviours which are typically not supported by the captive diet, then this mismatch could compromise welfare and result in FDB. Therefore, the weight of the evidence indicates that food handling, rather than food search (cf. McDonald Kinkaid, 2015), is the most likely predictor of FDB.

As already mentioned, other forms of oral SB (e.g. bar biting and repetitive tongue movements) have also been hypothesised to related to frustrated foraging behaviour in birds, including parrots (Keiper, 1969; Meehan et al., 2004). Oral SBs of orange-winged Amazon parrots were readily reduced when provided with foraging and other types of enrichments; and foraging enrichments successfully increased foraging times and reduced oral SBs in canaries, *Serinus canaria domestica* (Keiper, 1969). Despite this, McDonald Kinkaid (2015) found relative brain volumes rather than relative food search times to predict oral SBs; however, pooling distinct phases of foraging in the latter might result in reduced sensitivity to detect effects. Because of the links between frustrated foraging behaviour and oral SBs just described, it is therefore worthwhile re-examining wild foraging behaviour, specifically food handling time, as a risk factor for oral SBs.

McDonald Kinkaid (2015) found relative brain volumes to predict whole-body SBs in general, but this outcome pooled diverse forms of SB including route-tracing. Route-tracing relates to being widely ranging across Carnivora (see Chapters 2 and 3; Clubb and Mason, 2003; Clubb and Mason, 2007; Kroshko et al., 2016; with a similar trend reported in; Miller et al., 2018) and travel distances in Primates (Pomerantz et al., 2013). Good-quality equivalent data are rare for most parrot species (but see McFarland, 1991; Meyers, 1996; Greene and

Fraser, 1998; Bradbury et al., 2001; Salinas-Melgoza and Renton, 2005; Leech et al., 2008; Whitehead et al., 2011; Carneiro et al., 2012; Groom et al., 2015; Kennedy et al., 2015; Cliff et al., 2018), meaning that McDonald Kinkaid did not examine ranging behaviour as a risk factor for poor parrot welfare in her comparative study. However, searching for food is an important casual factor in how far a given species ranges (e.g. Clutton-Brock and Harvey, 1977b; McLoughlin and Ferguson, 2000; Rolando, 2002). So, if some species are motivated to perform food searching behaviours (e.g. as hypothesised in Chapter 3) creating a mismatch with the aforementioned spatial restrictions of captivity, this could compromise welfare (sensu Clubb et al., 2006), leading to route-tracing.

Based on the link between natural foraging behaviour and FDB uncovered by McDonald Kinkaid (2015), and other evidence I review above, here I test the following hypothesis:

i. Feather-damaging behaviour is linked with restriction of extensive oral manipulatory behaviours, or food handling time
    → *Prediction*: species whose wild diets require extensive oral manipulation should have more prevalent feather-damaging behaviour

As detailed above, McDonald (2015)'s analyses also revealed a risk factor for other SBs: relative brain volumes predicted prevalence of oral SBs and whole-body SBs. That different aspects of species-typical psittacine biology predict specific forms of abnormal behaviour may indicate that different motivational systems underlie these behaviours. If this is true, then *only* FBD should be predicted by this aspect of wild foraging behaviour i.e. other forms of SB should not be.

However, considering what I review above regarding oral SB and route-tracing, I also test the following hypotheses:

ii. Oral stereotypic behaviour is linked with restriction of extensive oral manipulatory behaviours, or food handling time

→ *Prediction*: species whose wild diets require extensive oral manipulation should have more prevalent oral stereotypic behaviour

iii. Route-tracing is linked with restriction of ranging behaviour associated with food search

→ *Prediction*: species whose wild diets require extensive food search should have more prevalent route-tracing

The second aim of this chapter is to investigate relationships between different types of whole-body SBs, and between these and oral SBs. In McDonald Kinkaid (2015)'s work, 'whole-body SBs' included diverse forms of SB, e.g. those involving active locomotion (e.g. route-tracing), movements around the bird's own axis (e.g. spinning), stationary whole-body movements (e.g. weaving and rocking), and those involving head-only movements (e.g. head-bobbing). Work on American mink, *Neovison vison* (Polanco et al., 2017; Polanco et al., 2018), and Primates (Pomerantz et al., 2013) indicate that some SBs are heterogenous, with different underlying causes. Thus while SBs in mink were historically pooled into a single behavioural category, there is strong evidence that scrabbling, whole-body and head-only SBs are distinct behaviours (Polanco et al., 2017). Scrabbling alone is affected by neighbour proximity, whereas the other two forms are reduced with enrichment provision (Polanco et al., 2018). Across Primates, hair-pulling is predicted by wild group sizes whereas route-tracing is predicted by wild daily travelling lengths (Pomerantz et al., 2013). In Carnivora, route-tracing specifically is predicted by large annual home range sizes (i.e. pooling route-tracing with other SBs weakens the effect: Kroshko et al., 2016). Therefore, pooling diverse forms of SB into one category may be inappropriate. However, because oral SBs and whole-body SBs share the same biological risk factor, McDonald Kinkaid (2015) suggested that despite outwardly appearing very different, they may be inter-related. In other words, potentially parrots' other forms of SB can be considered one and the same thing, and *ought* to be pooled into a single measure during analyses. Therefore, to better understand inter-relationships between different forms of SB and how they should be treated during analyses, I will explore relationships between them here. Finally, based on the outcome of hypothesis-testing and the inter-relationship analyses just described, the final aim of this chapter is to investigate whether foraging niche might explain any of the variance in other

SBs *not* explained by relative brain volumes (cf. McDonald Kinkaid, 2015; similar to the annual home range size models I ran in Section 3.2.5]).

4.2 Methods

4.2.1 Outcome and husbandry variable data collection

My outcome variables were published species-typical prevalence of FDB and oral SBs, calculated by McDonald Kinkaid (2015), and prevalence of four sub-types of whole-body SBs (route-tracing, spinning, stationary whole-body, and head-only SB) and all other SB (any form of non-FDB SB i.e. the five just mentioned) that I calculated. These were all calculated from survey responses of pet parrot owners (see Table 4.1 for definitions and Table 4.2 for values). Values describing 10 aspects of species-typical husbandry were also calculated from the same survey and used to control statistically for their effects where necessary (Section 2.4.4). Details of the survey are described in full by McDonald Kinkaid (2015), so I outline them briefly here. McDonald Kinkaid (2015)'s survey was created using SurveyMonkey software (www.surveymonkey.com) by her and Dr Yvonne van Zeeland, and was available in six languages (English, French, Dutch, Spanish, Greek, and Italian). An electronic advertisement was used to recruit participants (with links to the survey website: www.parrotsurvey.com), which was distributed by relevant organisations, institutions, and publications. This version featured 116 questions on parrot behaviour, demographics, rearing and current living conditions, and owner demographics. Participants identified their parrot's species from sets of coloured illustrations (taken, with the publisher's permission, from: Forshaw, 2010), to reduce the risk of unintentional owner-bias when reporting species identification. Participants with multiple parrots submitted one completed questionnaire per bird. All participants were at least 18 years old, neither names nor other identifying information (aside from e-mail addresses) were collected, and all data were confidentially stored on a secure server at Utrecht University. McDonald Kinkaid (2015) used responses made between April 2012–July 2013 to calculate her species-typical values.

Table 4.1 Calculation of species-level husbandry and abnormal behaviour outcome variables (adapted from McDonald Kinkaid, 2015). Given here are definitions and details of individual-level variables generated from the Parrot Survey responses, and for the subsequent species-typical behaviour and husbandry variables calculated from these. Stereotypic behaviours are listed, along with potential husbandry confounders that were later controlled for in analyses if required (see Section 4.2.5). Links between the potential confounders and stereotypic behaviours are indicated in the footnotes. FDB: feather-damaging behaviour; PCR: polymerase chain reaction; SB: stereotypic behaviour.

Individual-level variable	Definition	Variable levels or range	Species-level variable	Definition / calculation
Abnormal behaviour outcome variables				
FDB status	Does the parrot pluck, bite, or chew its own feathers?	Yes No	% FDB	Proportion of individuals with FDB (Yes v No)
Oral SB status	Does the parrot exhibit stereotypies[a] that involve the mouth? *Examples: chewing cage bars, moving up/down cage bars with beak, manipulating food/other items in mouth without chewing, moving tongue continuously*	Yes No	% Oral SB	Proportion of individuals that exhibit oral SB (Yes v No)

Individual-level variable	Definition	Variable levels or range	Species-level variable	Definition / calculation
Route-tracing status	Does the parrot exhibit stereotypies[a] that involve locomotion? *Examples: walking/climbing a set route*	Yes No	% Route-tracing	Proportion of individuals that exhibit route-tracing (Yes v No)
Spinning SB status	Does the parrot exhibit stereotypies[a] that involve rotation around the body's axis or around the perch? *Examples: e.g., pirouette or flips/circles around the perch (e.g., corner flip)*	Yes No	% Spinning SB	Proportion of individuals that exhibit spinning SB (Yes v No)
Stationary body SB status	Does the parrot exhibit stereotypies[a] that involve stationary whole-body movements? *Examples: weaving, bobbing and/or rocking*	Yes No	% Stationary body SB	Proportion of individuals that exhibit stationary body SB (Yes v No)
Head-only SB	Does the parrot exhibit stereotypies[a] that involve head-only movements?	Yes No	% Head-only SB	Proportion of individuals that exhibit head-only SB

Individual-level variable	Definition	Variable levels or range	Species-level variable	Definition / calculation
	Examples: head-bobbing or -twirling			(Yes v No)
All other SB	Does the parrot exhibit any form of stereotypy, excluding FDB?	Yes No	% All other SB	Proportion of individuals that exhibit any form of non-FDB SB (Yes v No)
Potential confounders: husbandry variables				
Age	Current developmental life stage	Adult Adolescent=*independent; full adult plumage; becoming sexually mature*	% Adult[c]	Proportion of individuals whose developmental stage is adult (v adolescent)
Sex 1	Sex: known or unknown; confirmed, if known, via DNA (PCR) analysis, endoscopy, or egg-laying	Known sex Unknown sex	% Known sex[d]	Proportion of individuals that are of known sex (v unknown sex)
Sex 2	Sex: female or male, among parrots of (confirmed) known sex	Female Male	% Female[e]	Proportion of individuals that are known females (v known males)

Individual-level variable	**Definition**	**Variable levels or range**	**Species-level variable**	**Definition / calculation**
Rearing	Mode of rearing, from hatch to weaning[b]	Human reared=*by humans only ("hand raised")* Parent reared=*by both humans and parrots, or by parrots only*	% Human reared[f]	Proportion of individuals that were human reared (v parent reared)
Housing	Main daytime housing	Standard cage=*~40x40x60cm* Larger=*cage ~ 80x50x100cm, or aviary, or other*	% Standard cage[g]	Proportion of individuals whose main daytime housing is a standard cage (v larger cage or enclosure)
Social contact	Social status, based on amount of regular contact with other parrots	Isolated=*no regular contact with other parrots* Social=*at least some regular contact with other parrots*	% Isolated[h]	Proportion of individuals whose social status is isolated (v social)

Individual-level variable	Definition	Variable levels or range	Species-level variable	Definition / calculation
Feeding time	Relative daily length of time typically spent feeding (foraging for and consuming food)	Short<*2 hours* Long≥*2 hours*	% Short feeding time[i]	Proportion of individuals who typically spend a relatively short time feeding daily (v long)
Captive diet diversity	Number of different types of food regularly offered	Six types: pellets, dried seeds/fruits/nuts, raw fruits/veg, egg food, table scraps, other	Captive diet diversity[j]	Median count of different types of food regularly offered (1-6)
Early enrichment diversity	Number of different types of stimulus regularly present in parrot's environment during the first year of life	Eight types: climbing/perching objects, toys, foraging devices, destructible items, hiding places, outdoor access, opportunities for flight, time outside cage	Early enrichment diversity[k]	Median count of different types of stimulus regularly present in a parrot's environment during the first year of life (0-8)
Current enrichment diversity	Number of different types of enrichment opportunity currently provided	Eight types: climbing/perching objects, toys, foraging devices, destructible items, hiding places, outdoor access,	Current enrichment diversity[k]	Median count of different types of enrichment opportunity currently provided (0-8)

Individual-level variable	Definition	Variable levels or range	Species-level variable	Definition / calculation
		opportunities for flight, time outside cage		

Footnotes

a. Stereotypic behaviours are apparently functionless behaviour sequences repeated according to a rigid pattern.

b. After weaning, the parrot is no longer being fed by its parent or caregiver, and is eating solid food on its own.

c. FDB is more common in adolescent or adult (v juvenile) parrots (Kinkaid et al., 2013); and FDB is suggested to be related to the onset of sexual maturity (Wedel, 1999).

d. Risk of FDB is higher in individuals of known (v unknown) sex (Kinkaid et al., 2013)

e. FDB is more prevalent in female (v male) parrots (Garner et al., 2006b; van Zeeland et al., 2009; Mellor, 2014)

f. Hand rearing is risk factor for stereotypic behaviours in grey parrots (Schmid et al., 2006)

g. Housing in cages that are "too small" or "too short" is a risk factor for SB in parrots and birds (Meehan et al., 2004; Leonard, 2005; Asher et al., 2009; van Zeeland et al., 2009; Polverino et al., 2012).

h. Isolation from conspecifics is a risk factor for SB in parrots (Meehan et al., 2003a; Leonard, 2005; van Zeeland et al., 2009).

i. Restricted opportunity to express foraging behaviour is a risk factor for SB parrots (Meehan et al., 2003b; van Zeeland et al., 2013); and FDB was both prevented and reduced in parrots provided with foraging and other enrichments (v non-enriched controls) (Meehan et al., 2003b).

j. Fresh fruits and vegetables in the captive diet influenced the relationship between species and FDB status in individuals (Kinkaid et al., 2013)

k. SB and FDB were prevented, or reduced, in parrots housed in enclosures with enrichments designed to offer foraging opportunities, exploration, locomotion, and physical complexity (v non-enriched controls) (Meehan et al., 2003b; Meehan et al., 2004).

At the beginning of my PhD, Dr Yvonne van Zeeland and I devised and added extra questions to the Parrot Survey to gain more detailed information on the foraging environment of respondents' parrots (see Appendix 4 for these; ethical approval for data collection was granted by the Faculty of Health Sciences Research Ethics Committee of the University of Bristol [University Investigation Number: 32441]). These extra questions were translated into the five extra languages the survey was originally available in (mentioned above), and the entire updated survey was translated into German. The updated version of the survey went live from September 2016, and until December 2017 I promoted the survey in several parrot-relevant Facebook groups and via Twitter. Data were later extracted from the survey software, and during processing it became apparent that an extraction error had occurred wherein some individuals and species present in McDonald Kinkaid (2015)'s dataset were missing from mine. As my deadline was approaching there was not enough time to re-extract and re-process these data again, and with this in mind I used McDonald Kinkaid (2015)'s dataset instead for my analyses.

4.2.1.1 Survey data processing

McDonald Kinkaid (2015)'s dataset had responses for 1,955 parrots from 74 species living across 47 countries. Two likely domesticated species, budgerigars, *Melopsittacus undulates*, and cockatiels, *Nymphicus hollandicus* (Bergman and Reinisch, 2006; Kalmar et al., 2010; Polverino et al., 2012), were excluded from analyses, because domestication results in animals phenotypically and genetically distinct from their wild ancestors or counterparts (Clutton-Brock, 1992; Driscoll et al., 2009). Birds of unknown species were also excluded, as were hybrids. As wild biology predictor variables generally represent adult or near adult behaviour, all chicks, juveniles, and those of unknown age were excluded, leaving records for 1,426 parrots (74 species). McDonald Kinkaid (2015) then used a series of SQL queries within stored procedures to collate data from a subset of relevant questions, subsequently yielding 13 variables for each parrot: three describing the presence or absence of FDB, whole-body SBs, and /or oral SBs; and ten 'husbandry' variables describing age, sex, rearing history, and other features of the captive environment (environmental enrichment and feeding regimes, cage size, and opportunities for social interaction) that were known to relate to the outcome variables. For my analyses investigating inter-relationships among SB

types, I returned to the unprocessed survey data and calculated five extra variables on the presence/absence of the four sub-types of whole-body SBs and all other SB (described in Table 4.1).

Data processing of individual-level survey responses to species-typical values are presented in Table 4.1. To ensure species-typical values were representative, species-typical values from those represented by <5 individuals were excluded (after Kroshko et al., 2016). The final dataset had species-typical stereotypic behaviour prevalence and corresponding husbandry values for up to 50 species per variable (Table 4.2).

4.2.2 Predictor variable data collation

Ideal predictor variables for each hypothesis would be direct measurements of each species' typical investment in performing food-search -handling behaviours (e.g. % active time searching for food; % active time spent manipulating food items). However, as experienced by McDonald Kinkaid (2015) such data are rarely reported in the literature. I therefore adopted McDonald Kinkaid (2015)'s method and based my predictor variables on indirect proxies (species-typical diet) which likely reflect species-typical effort associated with the two phases of appetitive foraging.

I used data on species-typical reliance of various dietary categories as reported in the avian EltonTraits foraging database (Wilman et al., 2014). This database provides percentages of species-typical reliance on nine dietary categories, of which the following were relevant for my species: invertebrates, fruit, nectar and pollen, seeds, and 'other' plant material (e.g. leaves, tubers, and bark). Briefly, Wilman et al. (2014) turned published dietary descriptions of species' diets into standardised semi-quantitative variables describing relative reliance on the dietary categories just described. To illustrate, if the published descriptions stated a given species as eating '*Mostly* fruit…', Wilman et al. (2014) scored it at least 60% for fruit in their database; if '*Sometimes* eats fruit…' they scored it as 10 or 20%; if '*Occasionally* eats fruit…' they scored it a maximum of 10%. Wilman et al. (2014)'s scores were adjusted based

on the rest of the account and its context, e.g. if described as '..eats *mostly* fruit and *sometimes* seeds and leaves…' the species would be scored as 60% for fruit, and 20% each for the other two within Wilman et al. (2014)'s database.

EltonTraits' authors pooled grass (and other small seeds, e.g. herbs) and tree seeds/nuts into a single category: percentage reliance on seeds. However, because I made opposing predictions about them regarding my hypotheses (see below) I referred back to Wilman et al. (2014)'s literature source for parrots (del Hoyo et al., 1997), and following their method as just described split their reported % reliance on seeds in their database proportionally between grass (and other small seeds, e.g. herbs) and tree seeds/nuts. Whilst reading through the literature source, I found one species' diet to have been recorded incorrectly in EltonTraits: black-headed parrot's entry, *Pionites melanocephalus,* had been coded as using 60% nectar, yet its account did not mention it using nectar but rather tree seeds. After corresponding with EltonTraits' authors (Y. Belmaker, pers. comm., 2020), I corrected its entry for my calculations of the following wild foraging predictor variables to reflect this (i.e. recorded it as 60% tree seeds).

a. Species-typical relative reliance on food requiring long search

Range: 0-100

This variable describes each species' % reliance on food items associated with a relatively long appetitive search phase, i.e. they require extensive search because they are patchily distributed in space and time and/or scarce or inconspicuous (originally based on: Mettke-Hofmann et al., 2002; Mettke-Hofmann et al., 2005; Mettke-Hofmann et al., 2012 by McDonald Kinkaid [2015] and which I adapted here). To calculate this variable I summed across each species' percentage reliance on the following categories, with justifications, to yield its relative *reliance on food requiring long search*. Note, I excluded from this calculation percentage reliance on 'other' plant material and grass seeds because these are quick to find, being conspicuous and abundant:

→ Invertebrates (namely insects and their larvae): inconspicuous

→ Nectar and pollen: patchily distributed in space and time, inconspicuous

→ Fruit: patchily distributed in space and time

→ Tree seeds/nuts: patchily distributed in space and time

Data were available for 50 species (see Table 4.2).

If my data support my route-tracing hypothesis (iii), then I expect a positive correlation between this and route-tracing prevalence.

b. Species-typical relative reliance on food requiring extensive oral manipulation

Range: 0-100

This variable describes each species' % reliance on food items associated with a relatively long handling times, i.e. they require extensive oral manipulation (originally based on: Mettke-Hofmann et al., 2002; Mettke-Hofmann et al., 2005; Mettke-Hofmann et al., 2012 by McDonald Kinkaid [2015] and which I adapted here). I summed across each species' percentage reliance on the following categories to calculate its *relative reliance on food requiring extensive oral manipulation.* Note, I excluded from this calculation percentage reliance on 'other' plant material, grass seeds, nectar and pollen, and fruit because these do not require extensive oral manipulation to access:

→ Invertebrates (namely insects and their larvae): larvae in particular require extensive oral manipulation, i.e. digging, to remove from the ground (e.g. Toft, 2015) or from tree trunks (e.g. Cameron, 2007)

→ Tree seeds/nuts: require extensive oral manipulation to access

Data were available for 50 species (see Table 4.2).

If my data support my FDB (i) and/or oral SBs (ii) hypotheses, then I expect a positive correlation between this and prevalence of these behaviours.

4.2.3 Investigating relationships among different forms of SB

As outlined in Section 4.1, the secondary aim of this chapter is to investigate relationships between different forms of whole-body SBs, oral SBs and FDB. Using the models described in Section 4.2.6 I investigated correlations between the four forms of whole-body SB I newly calculated (Section 4.2.1.1), oral SBs and FDB. If different SB forms positively correlate and share a biological risk factor, this would indicate species are affected by both forms suggesting they may have similar underlying causes (i.e. they should be pooled into a single measure for analyses) (cf. Polanco et al., 2017). If instead behaviours have different underlying causes then they should have different biological risk factors, and absent or negative correlations (indicating birds are doing one *or* the other) should be expected (i.e. subtypes should not be pooled for analyses) (cf. Polanco et al., 2017). Results of these models informed the analyses I describe next.

4.2.4 Relative brain volume analyses

McDonald Kinkaid (2015) found that species-typical relative brain volumes predicted other stereotypic behaviours (oral and whole-body SB prevalence). As mentioned above (Section 4.1), I recently replicated and confirmed this relationship using her data but using the same statistical methods describe here (see Section 4.2.6). I also confirmed that relative brain volumes do *not* predict FDB prevalence ($t_{4, 35}$=0.10, N=40, R^2=0.18, λ=0.67, P=0.92: McDonald Kinkaid et al., in prep.).

Like the models including annual home range size I ran in Chapter 3 for my Carnivora analyses (see Sections 3.2.5 and 3.3.3), I wanted to explore whether wild foraging explained any of the variance in other SB prevalence *not* explained by relative brain volumes. Once I had performed my hypothesis-testing models and also determined the most appropriate way to analyse the different forms of SB as mentioned above (i.e. as separate behavioural outcomes or pooled), I added each of my wild biology predictor variables to McDonald Kinkaid (2015)'s relative brain volume hypothesis-testing model (see Section 4.2.6 for details of the models used). I then assessed potential improvements to relative brain volumes using

its P value based on the t-statistic, and in model-fit overall using Adjusted R^2 values (Minitab Blog Editor, 2013).

4.2.5 Confound checks

Prior to hypothesis-testing I performed two checks. First, I investigated potential correlations between my wild foraging predictors, and between these and relative brain volumes. Where correlated predictors were identified, I ran additional models to check whether their inclusion affected interpretation of the model (in practice, they never did). Second, environmental conditions and demographics can also affect development of SBs and, if they correlate with my wild foraging predictors, could potentially confound my analyses (see Section 2.4.4). I therefore also assessed relationships between my two wild foraging predictor variables and the 10 aspects of species-typical husbandry calculated from the Parrot Survey data by McDonald Kinkaid (2015).

4.2.6 Statistical analyses

Statistical procedures were the same as per Chapter 3 (Section 3.2.7), with the following differences. For my predictor and husbandry confound checks, I constructed a parrot consensus tree from 1,000 BirdLife trees (Hackett backbone) (Jetz et al., 2012; Jetz et al., 2014), pruned to include only parrots, in 'phytools' (Revell, 2012). To account for phylogenetic uncertainty (see Section 2.4.7), all my final hypothesis-testing models, including the relative brain volume models, were performed over a tree block of the 1,000 alternative parrot phylogenetic trees (Jetz et al., 2012; Jetz et al., 2014), and results from these models are reported as medians and 95% CIs (shown in square parentheses).

4.3 Results

McDonald Kinkaid (2015)'s final dataset based on Parrot Survey responses included data on abnormal behaviour outcomes and corresponding living conditions for 1,378 parrots from up to 50 species per variable (see Table 4.2).

Table 4.2 Parrot comparative dataset used for analyses. Dashes indicate that either no data were available for a given species or, in the case of outcome and husbandry variables, that values came from fewer than five birds (see Section 4.2.1.1). Acronyms are as follows. Outcome variables: FDB=Feather-damaging behaviour prevalence. SB= all other stereotypic behaviour prevalence. RSB=route-tracing prevalence. SSB=spinning SB prevalence. WSB=stationary whole-body SB prevalence. HSB=head-only SB prevalence. OSB=oral SB prevalence. Wild biology predictor variables: RS=relative reliance on food requiring long search (%). RM=relative reliance on food requiring extensive oral manipulation (%). BV=brain volume (ml). BM=body mass (g). Potential husbandry confounders: DD=captive diet diversity (median, count). CE=current enrichment (median, count). EE=early enrichment (median, count). HR=proportion human-reared. PA=proportion adult. PC=proportion housed in a standard-sized cage. PF=proportion female. PI=proportion isolated. PK=proportion known sex. PS=proportion with short captive feeding times. See Section 4.2.1.1 and Table 6.1 for details on data processing and calculation of outcome and husbandry variables, and Section 4.2.2 for rationale and calculations of predictor variables.

		Outcome variables							*Wild biology predictors*				*Potential husbandry confounders*								
Species name	**Common name**	**FDB**	**SB**	**RSB**	**SSB**	**WSB**	**HSB**	**OSB**	**RS**	**RM**	**BV**	**BM**	**DD**	**CE**	**EE**	**HR**	**PA**	**PC**	**PF**	**PI**	**PK**	**PS**
Agapornis fischeri	Fischer's lovebird	0.00	0.20	0.00	0.20	0.20	0.20	0.20	20	0	1.95	48.30	4	7	6	-	0.80	0.40	-	0.20	0.60	0.20
Agapornis personatus	Yellow-collared lovebird	0.00	-	-	-	-	-	-	0	0	1.87	52.50	5	7	5	-	0.40	0.20	-	0.00	0.80	-
Agapornis roseicollis	Rosy-faced lovebird	0.23	0.17	0.10	0.05	0.02	0.07	0.15	35	35	1.86	45.80	4	6	5	0.04	0.84	0.32	0.37	0.14	0.86	0.35
Amazona aestiva	Blue-fronted Amazon	0.15	0.33	0.13	0.13	0.17	0.17	0.13	100	50	7.69	395.72	3	5	5	0.17	0.89	0.19	0.52	0.19	0.85	0.68
Amazona amazonica	Orange-winged Amazon	0.12	0.28	0.22	0.06	0.06	0.00	0.06	100	0	8.63	338.00	3.5	5	1.5	0.00	0.72	0.17	0.38	0.17	0.72	0.71
Amazona auropalliata	Yellow-naped Amazon	0.00	0.08	0.08	0.08	0.08	0.08	0.08	70	30	9.57	433.00	3	5.5	4	0.14	0.92	0.08	0.30	0.25	0.83	0.82
Amazona autumnalis	Red-lored Amazon	0.00	0.20	0.20	0.10	0.00	0.00	0.10	100	0	8.13	406.98	3	5.5	0	-	0.60	0.10	-	0.10	0.40	0.75
Amazona farinosa	Mealy Amazon	0.00	0.17	0.00	0.00	0.00	0.17	0.00	80	30	10.21	678.61	3	4.5	0	-	1.00	0.17	-	0.50	0.50	1.00
Amazona finschi	Lilac-crowned Amazon	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100	50	-	279.23	4	6	5	-	0.67	0.11	0.60	0.33	0.56	0.60
Amazona ochrocephala	Yellow-crowned Amazon	0.00	0.27	0.20	0.07	0.07	0.13	0.13	70	30	9.33	432.16	4	6	3	-	0.93	0.00	0.38	0.07	0.53	0.83
Amazona oratrix	Yellow-headed Amazon	0.08	0.25	0.17	0.00	0.17	0.08	0.00	70	30	8.62	433.00	4	6	5	0.17	0.85	0.08	0.58	0.31	0.92	0.70

		Outcome variables							***Wild biology predictors***				***Potential husbandry confounders***								
Species name	**Common name**	**FDB**	**SB**	**RSB**	**SSB**	**WSB**	**HSB**	**OSB**	**RS**	**RM**	**BV**	**BM**	**DD**	**CE**	**EE**	**HR**	**PA**	**PC**	**PF**	**PI**	**PK**	**PS**
Anodorhynchus hyacinthinus	Hyacinth macaw	0.22	0.22	0.22	0.00	0.00	0.00	0.22	100	0	24.97	1405.00	3	6	4	0.20	0.78	0.00	0.56	0.11	1.00	0.75
Ara ararauna	Blue-and-yellow macaw	0.11	0.39	0.16	0.07	0.20	0.23	0.25	70	30	17.90	1020.60	4	6	4	0.21	0.84	0.06	0.46	0.24	0.73	0.67
Ara chloropterus	Red-and-green macaw	0.17	0.38	0.05	0.00	0.14	0.14	0.14	70	30	22.17	1008.57	4	6	5	0.14	0.78	0.04	0.60	0.13	0.87	0.87
Ara macao	Scarlet macaw	0.13	0.22	0.00	0.00	0.11	0.22	0.22	70	30	19.14	915.30	4	5	4	0.00	0.67	0.00	0.25	0.22	0.89	0.83
Ara militaris	Military macaw	0.00	0.13	0.13	0.00	0.00	0.00	0.00	100	0	18.83	820.83	4	6	6	0.20	0.67	0.00	0.33	0.00	1.00	0.75
Ara rubrogenys	Red-fronted macaw	0.40	-	-	-	-	-	-	50	40	12.12	442.75	3	6	0	-	0.80	0.00	0.40	0.00	1.00	1.00
Ara severus	Chestnut-fronted macaw	0.09	0.27	0.09	0.00	0.00	0.09	0.09	80	50	9.83	387.72	4	6	3	-	0.91	0.00	0.33	0.18	0.82	0.50
Aratinga acuticaudata	Blue-crowned parakeet	0.18	0.18	0.00	0.00	0.18	0.09	0.09	90	40	5.50	166.50	4	7	4	0.00	1.00	0.08	0.50	0.08	0.67	0.45
Aratinga jandaya	Jandaya parakeet	0.00	0.00	0.00	0.00	0.00	0.00	0.00	80	0	-	103.88	3	5	5	-	0.86	0.43	0.50	0.00	0.86	1.00
Aratinga solstitialis	Sun parakeet	0.00	0.29	0.11	0.03	0.21	0.18	0.18	100	0	4.12	101.43	4	6	6	0.13	0.84	0.19	0.41	0.24	0.67	0.57
Bolborhynchus lineola	Barred parakeet	0.00	0.00	0.00	0.00	0.00	0.00	0.00	70	30	2.08	54.12	3	5.5	1.5	-	0.67	0.33	0.60	0.20	0.83	-
Cacatua alba	White cockatoo	0.45	0.38	0.30	0.09	0.15	0.11	0.26	100	100	14.16	631.00	3.5	6	3	0.22	0.91	0.13	0.44	0.16	0.91	0.64
Cacatua ducorpsii	Solomons cockatoo	0.67	0.50	0.13	0.13	0.25	0.25	0.25	80	50	8.70	415.00	4	7	5	-	0.56	0.22	0.80	0.22	0.56	0.56
Cacatua galerita	Sulphur-crested cockatoo	0.08	0.27	0.27	0.00	0.00	0.09	0.00	40	0	14.24	765.00	3	5	4	-	0.77	0.08	0.40	0.38	0.77	0.80
Cacatua goffiniana	Tanimbar cockatoo	0.53	0.40	0.20	0.10	0.20	0.13	0.23	30	10	-	-	4	5.5	0	0.40	0.88	0.15	0.58	0.12	0.71	0.68
Cacatua moluccensis	Salmon-crested cockatoo	0.52	0.37	0.33	0.07	0.07	0.19	0.19	100	50	15.63	850.00	3	6	1	1.00	1.00	0.00	0.48	0.20	0.93	0.68
Cacatua roseicapilla	Galah	0.22	0.19	0.14	0.05	0.10	0.10	0.10	0	0	6.43	351.00	4	6	5.5	0.29	0.83	0.13	0.48	0.09	0.96	0.33
Cacatua sanguinea	Little corella	0.00	0.60	0.20	0.00	0.20	0.20	0.20	10	10	8.91	437.50	4	5.5	0	-	1.00	0.33	0.40	0.17	0.83	0.83
Cacatua sulphurea	Yellow-crested cockatoo	0.33	0.44	0.17	0.11	0.39	0.39	0.28	100	50	9.62	344.00	4	6	0	0.11	0.94	0.11	0.33	0.17	0.83	0.53

		Outcome variables							***Wild biology predictors***				***Potential husbandry confounders***								
Species name	**Common name**	**FDB**	**SB**	**RSB**	**SSB**	**WSB**	**HSB**	**OSB**	**RS**	**RM**	**BV**	**BM**	**DD**	**CE**	**EE**	**HR**	**PA**	**PC**	**PF**	**PI**	**PK**	**PS**
Diopsittaca nobilis	Red-shouldered macaw	0.40	0.30	0.20	0.10	0.00	0.20	0.20	100	50	6.65	152.73	4	6	4	-	0.82	0.09	0.56	0.30	0.82	0.86
Eclectus roratus	Eclectus parrot	0.38	0.14	0.05	0.02	0.07	0.02	0.05	70	30	7.36	428.00	3.5	6	4	0.16	0.83	0.00	0.43	0.13	1.00	0.49
Forpus coelestis	Pacific parrotlet	0.14	0.16	0.11	0.00	0.05	0.05	0.05	50	0	1.34	29.18	3	6	5	0.14	0.67	0.29	0.00	0.38	0.95	0.32
Forpus passerinus	Green-rumped parrotlet	0.20	-	-	-	-	-	-	30	0	1.10	26.87	4	5.5	4	-	0.50	0.50	0.33	0.17	1.00	-
Myiopsitta monachus	Monk parakeet	0.09	0.50	0.23	0.10	0.10	0.37	0.30	55	25	4.08	108.63	4	6	4	0.15	0.91	0.28	0.33	0.34	0.66	0.71
Nandayus nenday	Nanday parakeet	0.13	0.25	0.00	0.00	0.13	0.13	0.25	60	30	4.93	116.60	4	6	4.5	-	1.00	0.05	0.60	0.13	0.63	0.29
Pionites leucogaster	White-bellied parrot	0.18	0.06	0.00	0.00	0.06	0.00	0.06	100	60	5.11	155.00	3	6	6	-	0.94	0.12	0.56	0.06	0.94	0.44
Pionites melanocephalus	Black-headed parrot	0.20	0.20	0.20	0.07	0.13	0.07	0.20	150	60	5.30	146.55	3.5	7	1	0.20	0.71	0.00	0.44	0.13	0.94	0.50
Pionus menstruus	Blue-headed parrot	0.00	0.36	0.18	0.00	0.00	0.09	0.27	70	40	5.78	250.79	3	6	5	0.00	0.83	0.42	0.56	0.17	0.75	0.80
Pionus senilis	White-crowned parrot	0.00	0.13	0.13	0.13	0.00	0.00	0.00	100	50	-	212.68	2.5	6	2	-	0.88	0.00	0.83	0.13	0.75	-
Poicephalus gulielmi	Red-fronted parrot	0.20	0.00	0.00	0.00	0.00	0.00	0.00	70	40	5.80	213.50	3	4	5	-	1.00	0.20	-	0.20	0.80	0.60
Poicephalus meyeri	Meyer's parrot	0.16	0.22	0.17	0.11	0.17	0.17	0.11	70	40	4.41	117.50	3	6	3	0.10	0.86	0.14	0.65	0.05	0.81	0.54
Poicephalus rufiventris	Red-bellied parrot	0.00	0.14	0.00	0.00	0.14	0.14	0.00	100	50	-	-	3.5	6.5	6	0.00	1.00	0.13	0.63	0.00	1.00	0.67
Poicephalus senegalus	Senegal parrot	0.16	0.19	0.04	0.02	0.11	0.09	0.09	70	30	4.71	155.00	3	6	4	0.09	0.89	0.23	0.48	0.18	0.77	0.62
Primolius auricollis	Yellow-collared macaw	0.50	0.17	0.17	0.00	0.17	0.17	0.17	100	50	8.09	212.67	4	6	0	-	1.00	0.00	0.40	0.00	0.83	0.83
Psittacula eupatria	Alexandrine parakeet	0.00	0.33	0.17	0.00	0.17	0.00	0.17	70	10	5.54	214.00	3	5	2.5	-	1.00	0.17	0.50	0.17	1.00	0.50
Psittacula krameri	Rose-ringed parakeet	0.08	0.25	0.25	0.00	0.00	0.00	0.00	70	10	3.90	137.00	3	6	4	0.50	0.92	0.17	0.36	0.17	0.92	1.00
Psittacus erithacus	Grey parrot	0.37	0.18	0.10	0.03	0.09	0.08	0.09	100	50	9.18	405.50	4	6	4	0.16	0.76	0.07	0.47	0.27	0.77	0.62
Pyrrhura frontalis	Maroon-bellied parakeet	0.14	0.00	0.00	0.00	0.00	0.00	0.00	70	40	2.95	80.26	4	6	6	-	0.71	0.14	0.60	0.29	0.71	0.60
Pyrrhura molinae	Green-cheeked parakeet	0.10	0.32	0.20	0.00	0.02	0.22	0.29	80	20	-	64.80	4	7	5	0.00	0.74	0.30	0.57	0.26	0.53	0.50

4.3.1 Descriptive statistics

Overall, 25% of parrots performed one or more forms of other SB, and 21% of birds were affected by FDB (McDonald Kinkaid et al., in prep.). Of the four subtypes of whole-body SB, route-tracing was most prevalent at 14%, head-only SBs had a prevalence of 11%, stationary whole-body SBs affected 10% of individuals, and spinning SBs were the least prevalent at 4%. Oral SBs had a prevalence of 13% (McDonald Kinkaid et al., in prep.).

Species' prevalence of abnormal behaviour outcome variables are shown in Table 6.2. Five species did not perform any SB (e.g. maroon-bellied parakeets, *Pyrrhura frontalis*), whereas the species with most prevalent SB were little corellas, *Cacatua sanguinea* (60%). Considering FDB, little corellas are one of the species least affected (0%), whereas Solomons cockatoos, *Cacatua ducorpsii* (67%), were most affected (McDonald Kinkaid et al., in prep.). For route-tracing, 12 species had a prevalence of 0%, e.g. lilac-crowned parrots, *Amazona finschi*, whereas 33% of salmon-crested cockatoos, *Cacatua moluccensis*, route-traced. 13 species were unaffected by head-only SBs (e.g. Alexandrine parakeet, *Psittacula eupatria*), and the species most affected by this SB were yellow-crested cockatoos, *Cacatua sulphurea* (39%). 15 species did not perform stationary whole-body SBs, whereas 39% of yellow-crested cockatoos did. Finally, spinning SBs were the rarest: nearly half (24/50) of species had a prevalence of 0% (e.g. barred parakeets, *Bolborhynchus lineola*). The species with the most prevalent spinning SBs was Fischer's lovebirds, *Agapornis fischeri* (20%). Species such as rose-ringed parakeets, *Psittacula krameria*, had the least prevalent oral SBs (0%), and the monk parakeet, *Myiopsitta monachus,* the most (30%) (McDonald Kinkaid et al., in prep.).

4.3.2 Results of confound checks

My two wild foraging predictor variables and relative brain volumes all significantly related to one another (see Table 4.3). Species with relatively large brains are relatively more reliant on wild food requiring long food search (t_{41}=3.038, N=44, R^2=0.242, λ=0.461, P=0.004), and vice versa (t_{41}=2.924, N=44, R^2=0.960, λ=0.739, P=0.006). Species relatively more reliant on wild food requiring long food search are also reliant on those requiring extensive oral

manipulation (t_{48}=3.285, N=50, R^2=0.184, λ=0, P=0.002) and vice versa (t_{48}=3.055, N=50, R^2=0.163, λ=0.365, P=0.004).

As detailed in Section 4.2.5, including correlated predictors never affected the interpretation of the model with the focal predictor; thus, they were not included in any final hypothesis-testing models.

The following aspects of species-typical husbandry were found to correlate with my wild foraging behaviour predictor variables (see Table 4.4). Species relatively more reliant on wild food requiring long food search are less likely to be housed in standard-sized cages (t_{47}=-2.841, N=49, R^2=0.147, λ=0, P=0.007), and also have less diverse captive diets (t_{48}=-2.269, N=50, R^2=0.097, λ=0, P=0.028). Species relatively more reliant on wild food requiring extensive oral manipulation are more likely to be adult (t_{48}=3.121, N=50, R^2=0.169, λ=0, P=0.003), female (t_{43}=2.500, N=44, R^2=0.127, λ=0, P=0.016), and less likely to be housed in a standard-sized cage (t_{48}=-2.038, N=50, R^2=0.080, λ=0, P=0.047). Regarding relative brain volume, my recent reanalysis of McDonald Kinkaid (2015)'s work using PGLS revealed that relatively larger-brained species are less likely to be housed in standard cages (t_{41}=-3.82, N=44, R^2=0.57, λ=0, P<0.001) (McDonald Kinkaid et al., in prep.).

These aspects of husbandry were thus included as additional predictor terms in the relevant hypothesis-testing models.

Table 4.3 Results of PGLS models of between-predictor checks. During hypothesis-testing, additional models were performed including these correlated predictors as additional terms to assess their potential effects on the focal predictor (see Section 4.2.5). As correlated predictors never affected the interpretation of the focal one, correlated predictors were not included in final hypothesis-testing models. Results are considered significant at P<0.05 and shown in bold, trends (P<0.10) are italicised, and reported to three decimal places.

Outcome: / **Predictor:**	**Relative reliance on wild food requiring long search appetitive search phase length**	**Relative reliance on wild food requiring extensive oral manipulation**	**Brain volume***
Relative reliance on wild food requiring long search appetitive search phase length		**t_{48}=3.285, N=50, R^2=0.184, λ=0, P=0.002**	**t_{41}=2.924, N=44, R^2=0.960, λ=0.739, P=0.006**
Relative reliance on wild food requiring extensive oral manipulation	**t_{48}=3.055, N=50, R^2=0.163, λ=0.365, P=0.004**		*t_{41}=1.708, N=44, R^2=0.953, λ=0.773, P=0.095*
Brain volume*	**t_{41}=3.038, N=44, R^2=0.242, λ=0.461, P=0.004**	*t_{40}=2.001, N=43, R^2=0.104, λ=0, P=0.052*[a]	

* Body mass included in all models to control for allometric effects. Outlier removed: [a] *Cacatua alba*

Table 4.4 Results of PGLS models investigating correlations between my two wild foraging predictor variables and species-typical husbandry. Results are considered significant at P<0.05 and shown in bold, and given to three decimal places. During hypothesis-testing, correlated husbandry variables were included in final models. Prop.=proportion; med.=median; Stand.=standard. Results are considered significant at P<0.05 and shown in bold, and reported to three decimal places

Outcome: **Predictor:**	**Prop. adult**	**Prop. known sex**	**Prop. female**	**Prop. human reared**	**Prop. in stand. cage**	**Prop. isolated**	**Prop. short feed times**	**Captive diet diversity**	**Med. early EE score**	**Med. current EE score**
Relative reliance on wild food requiring long search	t_{47}=1.474, N=49, R^2=0.044, λ=0, P=0.147[a]	t_{48}=-0.454, N=50, R^2=0.004, λ=0, P=0.652	t_{43}=1.581, N=45, R^2=0.055, λ=0, P=0.121:	t_{26}=-0.223, N=28, R^2=0.002, λ=0.203, P=0.826	**t_{47}=-2.841, N=49, R^2=0.147, λ=0, P=0.007[b]**	t_{48}=0.054, N=50, R^2<0.001, λ=0, P=0.957	t_{43}=1.382, N=45, R^2=0.043, λ=0, P=0.174[c]	**t_{48}=-2.269, N=50, R^2=0.097, λ=0, P=0.028**	t_{48}=-0.629, N=50, R^2<0.001, λ=0.051, P=0.532	t_{48}=-0.258, N=50, R^2=0.001, λ=0, P=0.797
Relative reliance on wild food requiring extensive oral manipulation	**t_{48}=3.121, N=50, R^2=0.169, λ=0, P=0.003**	t_{48}=-0.001, N=50, R^2<0.001, λ=0, P=0.999	**t_{43}=2.500, N=44, R^2=0.127, λ=0, P=0.016**	t_{26}=-0.562, N=28, R^2=0.012, λ=0.231, P=0.579	**t_{48}=-2.038, N=50, R^2=0.080, λ=0, P=0.047**	t_{48}=0.365, N=50, R^2=0.003, λ=0, P=0.717	t_{43}=0.078, N=45, R^2<0.001, λ=0, P=0.938[c]	t_{48}=0.149, N=50, R^2<0.001, λ=0.405, P=0.882	t_{48}=-1.035, N=50, R^2=0.022, λ=0.025, P=0.306	t_{48}=0.906, N=50, R^2=0.017, λ=0, P=0.370

Outliers removed: [a]*Agapornis personatus*; [b]*Diopsittaca nobilis*; [c]*Poicephalus meyeri*

4.3.3 Hypothesis-testing results

Hypothesis-testing models were performed over a tree block (see Section 4.2.6), so median values for each parameter are shown here with their 95% CIs given in square parentheses (for full results see Table 4.5).

After controlling for husbandry, species reliant on wild food requiring extensive oral manipulation (i.e. long food handling times) have more prevalent FDB (t_{40}=2.415 [2.413, 2.417], N=45, R^2=0.214 [0.214, 0.214], λ=0.329 [0.328, 0.330], P=0.020 [0.020, 0.020]) (see Figure 4.2). All other models, including those with route-tracing and oral SBs as outcomes, were non-significant (see Table 4.5).

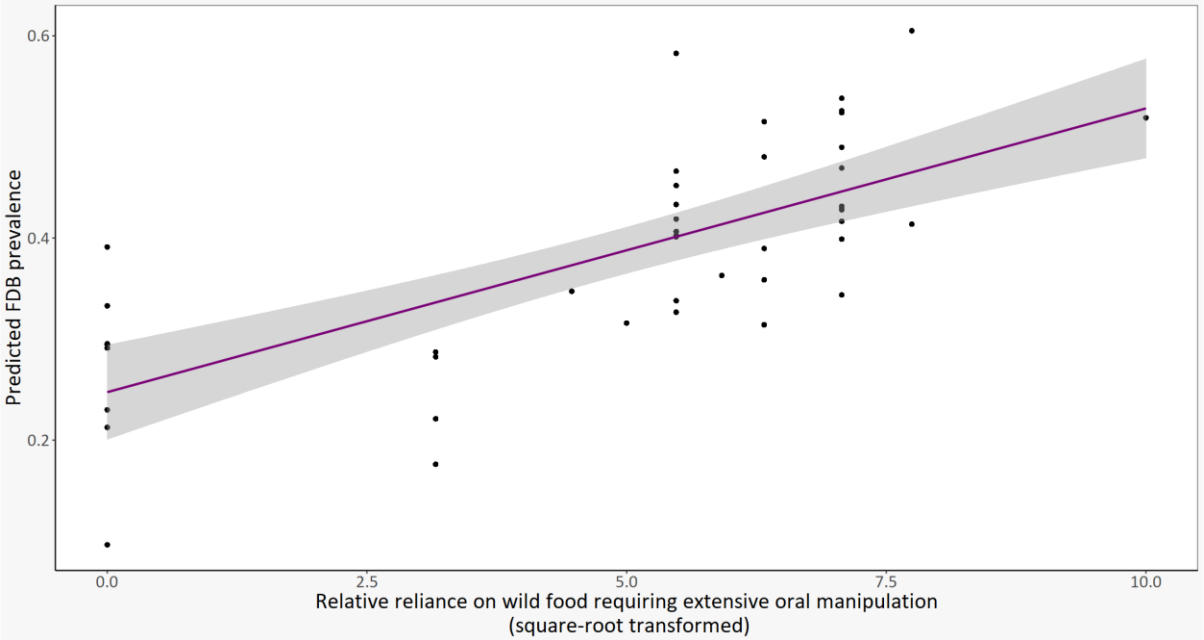

Figure 4.2 Relationship between species-typical relative reliance on wild food requiring extensive oral manipulation and feather-damaging behaviour (FDB) prevalence. The shaded area shows the 95% confidence region. Note that because this model had multiple terms, predicted values of FDB are shown on the Y axis. Species relatively more reliant on wild food require extensive oral manipulation have more prevalent FDB (median parameters and [95%CIs]: t_{40}=2.415 [2.413, 2.417], N=45, R^2=0.214 [0.214, 0.214], λ=0.329 [0.328, 0.330], P=0.020 [0.020, 0.020]).

In line with the idea that FDB and other SBs share different underlying motivational bases (cf. McDonald Kinkaid, 2015), prevalence of other SBs were not predicted by relative reliance on food requiring extensive manipulation (nor my other my wild foraging predictor variable; see Table 4.5).

Table 4.5 Results of PGLS models performed over a tree block of 1,000 alternative Psittaciform trees, assessing relationships between my two wild foraging predictor variables and three outcome variables, prevalence of feather-damaging behaviour (FDB), oral stereotypic behaviours (SB), and route-tracing. The fourth outcome, prevalence of all other SB (see Section 4.2.3), relates to my prediction that if FBD and other forms of SB have different motivational bases, they should not share biological risk factors (see Section 4.1). Previously identified potentially confounding aspects of species-typical husbandry are included where applicable. Model parameters are summarised as medians, with 95% confidence intervals given in square parentheses. t and P values correspond to the focal wild biology predictor. Results are considered significant at P<0.05, shown in bold where applicable, and reported to three decimal places.

Outcome	Wild biology predictor	Husbandry controlled for	t	df	N	R^2	λ	P
FDB	Relative reliance on food requiring long search	Proportion in standard cage Captive diet diversity	0.825 [0.822, 0.828]	46	50	0.089 [0.089, 0.089]	0.300 [0.298, 0.301]	0.414 [0.412, 0.416]
FDB	**Relative reliance on food requiring extensive oral manipulation**	**Proportion adult** **Proportion female** **Proportion in standard cage**	**2.415 [2.413, 2.417]**	**40**	**45**	**0.214 [0.214, 0.214]**	**0.329 [0.328, 0.330]**	**0.020 [0.020, 0.020]**

Outcome	Wild biology predictor	Husbandry controlled for	t	df	N	R^2	λ	P
Oral SB	Relative reliance on food requiring long search	Proportion in standard cage Captive diet diversity	0.386 [0.382, 0.389]	43	47	0.165 [0.165, 0.165]	0.016 [0.015, 0.017]	0.701 [0.699, 0.705]
Oral SB	Relative reliance on food requiring extensive oral manipulation	Proportion adult Proportion female Proportion in standard cage	1.543 [1.537, 1.548]	38	43	0.103 [0.103, 0.104]	0.003 [0, 0.006]	0.131 [0.130, 0.1326]
Route-tracing	Relative reliance on food requiring long search	Proportion in standard cage Captive diet diversity	0.796 [0.793, 0.799]	43	47	0.048 [0.048, 0.048]	0.340 [0.337, 0.342]	0.430 [0.429, 0.432]
Route-tracing	Relative reliance on food requiring	Proportion adult	-0.940 [-0.943, -0.937]	38	43	0.072 [0.072, 0.073]	0.322 [0.320, 0.325]	0.353 [0.352, 0.354]

Outcome	Wild biology predictor	Husbandry controlled for	t	df	N	R^2	λ	P
	extensive oral manipulation	Proportion female Proportion in standard cage						
All other SB	Relative reliance on food requiring long search	Proportion in standard cage Captive diet diversity	0.268 [0.266, 0.271]	43	47	0.110 [0.110, 0.110]	0.381 [0.380, 0.382]	0.790 [0.787, 0.792]
All other SB	Relative reliance on food requiring extensive oral manipulation	Proportion adult Proportion female Proportion in standard cage	0.517 [0.516, 0.520]	38	43	0.067 [0.067, 0.067]	0.318 [0.317, 0.319]	0.608 [0.606, 0.609]

4.3.4 Correlations between different forms of SB

Results of analyses examining potential correlations between the four sub-types of whole-body SBs, oral SBs and FDB are shown in Table 4.6. Only oral SBs significantly positively correlated with route-tracing. Spinning, head-only, and oral SBs, and FDB all significantly positively correlated with stationary whole-body SBs. Stationary whole-body, head-only, and oral SBs all significantly positively correlated with spinning SBs, and route-tracing and FDB tended to. Stationary whole-body, spinning, and oral SBs all significantly positively correlated with head-only SBs, and FDB tended to. All forms of other SB and FDB significantly positively correlated with oral SBs. Oral SBs significantly positively correlated with FDB, and spinning and stationary whole-body SBs tended to.

In sum, all four subtypes of whole-body SB significantly positively correlated with at least one other subtype, and/or positively correlated with oral SB prevalence. Because neither oral SBs nor route-tracing related to either of my wild foraging niche predictors (yet FDB did to one of them; see Table 4.5), and that McDonald Kinkaid (2015) found whole-body SB and oral SB prevalence to share the same biological risk factor (relative brain volumes), this supports that these outwardly different forms of other SB may be considered different responses for the same underlying challenge (sensu McDonald Kinkaid et al., in prep.). Thus, the most parsimonious approach is to pool these behaviours into a single behavioural outcome measure, i.e. 'all other SB', for my upcoming statistical analyses (Section 4.2.3; see also Table 4.1).

FDB's relationship with the subtypes of other SB was weaker and less consistent (e.g. R^2 values all ≤0.127; see Table 4.6). FDB also has a different biological risk factor (reliance on foods requiring extensive oral manipulation, Section 4.3.3; and cf. McDonald Kinkaid, 2015), indicating that FDB is distinct from other SBs (also in agreement with: Garner et al., 2006a) and may have a different motivational basis. Thus, it is most appropriate to continue to analyse it separately from other SBs. Figure 4.3 displays the consensus phylogenetic tree of the species in my analyses, along with their values for FDB and all other SB prevalence.

Table 4.6 Results of PGLS models investigating potential relationships between different forms of stereotypic behaviours (SB) involving the body, oral SBs and feather-damaging behaviour (FDB). Results are considered significant at P<0.05 and shown in bold, italics indicate trends (at P<0.10), and all are reported to three decimal places.

Outcome: Predictor:	**Route-tracing**	**Spinning SBs**	**Stationary whole-body SBs**	**Head-only SBs**	**Oral SBs**	**FDB**
Route-tracing		*t_{45}=1.966, N=47, R^2=0.079, λ=0, P=0.056*	t_{45}=-0.056, N=47, R^2<0.001, λ=0.115, P=0.956	t_{45}=1.422, N=47, R^2=0.043, λ=0, P=0.162	**t_{45}=2.961, N=47, R^2=0.163, λ=0, P=0.005**	t_{45}=1.217, N=47, R^2=0.032, λ=0.278, P=0.230
Spinning SBs	t_{45}=1.497, N=47, R^2=0.047, λ=0.273, P=0.141		**t_{45}=2.681, N=47, R^2=0.138, λ=0.087, P=0.010**	**t_{45}=3.101, N=47, R^2=0.176, λ=0, P=0.003**	**T_{45}=2.841, N=47, R^2=0.152, λ=0.180, P=0.008**	*t_{45}=1.784, N=47, R^2=0.066, λ=0.385, P=0.081*
Stationary whole-body SBs	t_{45}=-0.376, N=47, R^2=0.003, λ=0.335, P=0.709	**t_{45}=2.823, N=47, R^2=0.150, λ=0, P=0.007**		**t_{45}=4.962, N=47, R^2=0.354, λ=0, P<0.001**	**t_{45}=3.985, N=47, R^2=0.261, λ=0, P<0.001**	*t_{45}=1.691, N=47, R^2=0.060, λ=0.268, P=0.098*

Outcome: **Predictor:**	**Route-tracing**	**Spinning SBs**	**Stationary whole-body SBs**	**Head-only SBs**	**Oral SBs**	**FDB**
Head-only SBs	t_{45}=0.891, N=47, R^2=0.017, λ=0.285, P=0.378	**t_{45}=2.991, N=47, R^2=0.166, λ=0.159, P=0.004**	**t_{45}=5.600, N=47, R^2=0.411, λ=0, P<0.001**		**t_{45}=5.772, N=47, R^2=0.425, λ=0, P<0.001**	t_{45}=1.180, N=47, R^2=0.030, λ=0.229, P=0.244
Oral SBs	**t_{45}=2.669, N=47, R^2=0.137, λ=0.269, P=0.011**	**t_{45}=2.875, N=47, R^2=0.155, λ=0.241, P=0.006**	**t_{45}=3.872, N=47, R^2=0.250, λ=0.062, P<0.001**	**t_{44}=5.008, N=46, R^2=0.363, λ=0, P<0.001[a]**		**t_{45}=2.101, N=47, R^2=0.089, λ=0.181, P=0.041**
FDB	t_{45}=1.284, N=47, R^2=0.035, λ=0.229, P=0.206	*t_{45}=1.823, N=47, R^2=0.069, λ=0, P=0.075*	**t_{45}=2.377, N=47, R^2=0.112, λ=0, P=0.022**	*t_{45}=1.901, N=47, R^2=0.074, λ=0, P=0.064*	**t_{45}=2.558, N=47, R^2=0.127, λ=0, P=0.014**	

Outlier removed: [a]*Pyrrhura frontalis*

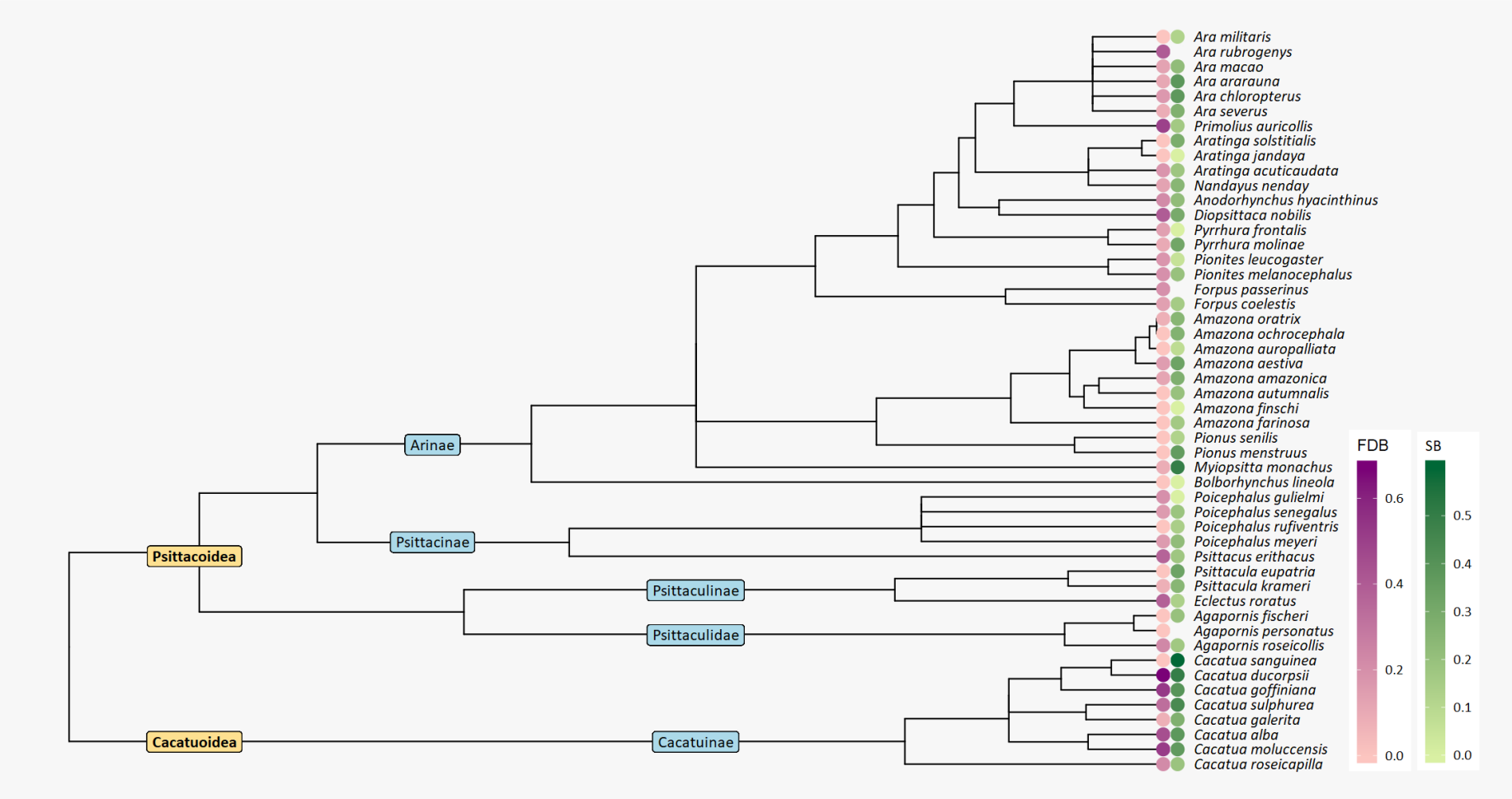

Figure 4.3 Phylogenetic tree of the 50 parrot species featured in my analyses. Species' feather-damaging behaviour (FDB) all other stereotypic behaviour (SB) prevalence is shown as tip points and coloured according to value (lighter colour representing lower prevalence; darker representing higher). Missing tip points indicate that no useable data were available for that species. Superfamily names are shown in yellow labels and family or subfamily names are shown in blue.

4.3.5 Results of relative brain volume models

Adding my two wild foraging predictor variables to McDonald Kinkaid et al. (in prep.)'s relative brain mass model with all other SB prevalence as the outcome did not improve the fit of these models (see Table 4.7).

Table 4.7 Results of PGLS models adding my two wild foraging predictor variables as additional terms to McDonald Kinkaid et al. (in prep.)'s relative brain volume hypothesis-testing model. On the left is the relative brain volume – the t and associated P value relate to brain volume. On the right are the results of models including, in turn, my two wild foraging predictors (i and ii). For these, the t and P values for brain volume and for the wild foraging predictor are provided, along with whole model parameters. Under 'Interpretation' based on the model's Adjusted (Adj.) R^2 and brain volume's P values I determine the effect of each foraging niche predictor. Models were ran over a tree block of 1,000 alternative Psittaciform trees, and parameters are summarised as medians, with 95% confidence intervals given in square parentheses. Results are considered significant at P<0.05, shown in bold where applicable, and reported to three decimal places.

McDonald Kinkaid et al. (in prep.)'s relative brain volume model*		***Models including my wild foraging variables as additional terms***			
Outcome	**Relative brain volume result**	**Predictors**	**Predictor parameters**	**Whole model parameters**	**Interpretation**
All other SB	**t_{37}=2.591 [2.588, 2.594], N=41, Adj. R^2=0.245 [0.245, 0.245], λ=0.330 [0.328, 0.332], P=0.014 [0.014, 0.014]**	Relative brain volume *and* i) Relative reliance on wild food requiring long search	**t=2.606 [2.604, 2.609], P=0.012 [0.012, 0.012]** t=-0.588 [-0.589, -0.586], P=0.560 [0.559, 0.562]	i) $F_{4, 36}$=4.065 [4.058, 4.073], N=41, Adj. R^2=0.235 [0.234, 0.235], λ=0.299 [0.298, 0.302]	Adj. R^2 ↓ Brain vol.'s P slightly ↓ *No improvement*
		Relative brain volume *and* ii) Relative reliance on wild food requiring extensive oral manipulation	**t=2.454 [2.451, 2.457], P=0.019 [0.019, 0.019]** t=0.403 [0.400, 0.406], P=0.689 [0.687, 0.692]	ii) $F_{4, 36}$=3.915 [3.908, 3.921], N=41, Adj. R^2=0.226 [0.225, 0.226], λ=0.345 [0.343, 0.347]	Adj. R^2 ↓ Brain vol.'s P slightly ↑ *No improvement*

* body mass is included in all models to control for allometric effects, as is a husbandry confounder (proportion of birds housed in a standard cage)

4.4 Discussion

In this chapter, I found support for my hypothesis that feather-damaging behaviour is linked with reliance on wild food requiring extensive oral manipulation or, in other words, long food handling times. Thus, this can be considered a biological risk factor for FDB. I did not find support for my other hypotheses, relating other oral SBs to the same aspect of foraging just mentioned, and route-tracing with reliance on wild food requiring long search. I also confirmed support for the idea that FDB and other forms of SB have different underlying motivational bases: FDB's biological risk factor did not predict prevalence of all other forms of SB (also cf. McDonald Kinkaid, 2015) and *vice versa* (McDonald Kinkaid et al., in prep.). Regarding the secondary aim of my chapter, I found that outwardly different forms of non-FDB SBs are likely related responses to captivity's challenges, and that pooling them into a single 'all other SB' behavioural outcome measure is most appropriate for analyses. For my final aim, adding my two wild foraging predictor variables did not explain variance in other SBs not explained by relative brain volumes (cf. McDonald Kinkaid et al., in prep.). These final findings further support that FDB is distinct from other forms of SB in parrots, with different underlying motivational systems (also see McDonald Kinkaid et al., in prep.). Next, I outline the limitations of my study, then discuss my hypothesis-testing results and associated recommendations.

Limitations of my study might include generalisability. My sample size (up to 50 species) is larger than those of Chapters 3 and 5 (maximum 27 species and 13 species, respectively), and well over the 20 minimum recommended by Blomberg et al. (2003) (see also Section 2.4.2). However, my sample is not a random one of all ~400 extant Psittaciformes currently recognised (IUCN, 2019): one of the superfamilies is entirely unrepresented (Strigopoidea) as are some subfamilies (e.g. Loriinae and Platycercinae). Strigopoidea includes three species: the kea, *Nestor notabilis*, kaka*, N. meridionalis*, and the flightless kakapo, *Strigops habroptila*, all native to New Zealand; while Loriinae and Platycercinae are specious subfamilies native to Australasia (Wright, 2015). Potentially, there may be something about the biology of these species meaning they are less common or never kept as pets, e.g. deemed less attractive (Vall-llosera and Cassey, 2017), or because they have dietary or other

requirements that are difficult to cater for, e.g. many of the Loriinae are nectarivores (Toft, 2015). As making welfare recommendations for *pet* parrots, rather than all parrots, is my aim it is likely that my sample *is* representative of this subset of parrots, i.e. those commonly kept in captivity. Additionally, my outcome and husbandry data are owner-reported, so may be biased toward people already actively aware of their bird's welfare and interested in improving it. Survey responses from multiple people may also introduce noise into my dataset (see Section 2.4.3.2). Finally, I cannot rule out that there may be some unmeasured dietary characteristic, such as nutritional content, that systematically varies among the diet types I used to calculate my wild foraging predictors, which may provide an alternative explanation for my result (cf. McDonald Kinkaid, 2015). I discuss this in detail next.

4.4.1 FDB result

As just mentioned, I cannot state what the casual explanation is for my FDB result. However, I can propose two types of explanation which could be teased apart experimentally: i) differences between wild and captive diets in food handling times and oral manipulation, and ii) differences in nutritional content. Firstly, as assumed here, FDB might result from the mismatch (sensu Section 1.1) between wild and captive food handling times or effort, resulting in oral attention being redirected to feathers (i.e. a motivated behaviour pattern being redirected to an inappropriate substrate [feathers], e.g. Fraser et al., 1997). If so, it supplies the following testable predictions: i) that species most reliant on wild foods requiring extensive oral manipulation should spend the most time performing FDB; ii) naturalising captive food handling times to more closely mimic wild ones should reduce FDB; and iii) that FDB would initially develop in the context of feeding and/or temporally close to feeding bouts. Experimental work holding nutritional content of pellets constant whilst varying the manipulation effort required to consume them, found that oversized pellets were strongly preferred over regular-sized ones, and foraging times were also increased (Rozek et al., 2010; Rozek and Millam, 2011). This would indirectly indicate that handling times and oral manipulation behaviour *per se* might relate to FDB.

Remaining with the theme of FDB relating to oral manipulation, is that in humans and other animals there are links between chewing and cognitive function. Reduced mastication is associated with loss of cognitive function, including memory loss and reduced learning ability (Kubo et al., 2013; Krishnamoorthy et al., 2018; Weijenberg et al., 2019). One possible mechanism behind this relationship, is that mastication itself provides sensory input to the central nervous system, so reduced levels may lead to decreased neural activity (Kubo et al., 2013; Krishnamoorthy et al., 2018; Weijenberg et al., 2019). If FDB is redirected food-related oral attention, and if even *with* FDB birds masticate for less time or with less effort than is biologically normal, then one would predict that affected birds would likewise show reduced cognitive function. A second mechanism, is that chewing during stressful situations can be a coping mechanism, alleviating effects of chronic stress, e.g. susceptibility to disease and impaired learning (Kubo et al., 2013; Krishnamoorthy et al., 2018; Weijenberg et al., 2019), which seems potentially biologically relevant to FDB and parrots. As mentioned above, for parrots a lack of appropriate chewing substrate in the captive diet might result in chewing being directed to the feathers. If this is the case, then one would predict that signs of acute stress, e.g. heart rate, should be lower during and immediately after a bout of FDB (after Novak, 2003). For affected birds, preventing birds from performing FDB should result in *increased* signs of acute and chronic stress in the short- and long-term, and would therefore directly compromise welfare (sensu Mason and Latham, 2004). Under this scenario, providing plentiful chewing substrates to parrots, especially those with the biological risk factor here (Table 4.2) from an early age is an easily implemented enrichment that might help prevent FDB development

Alternatively, FDB might instead relate to *nutritional differences* between wild and captive diets, that covary with manipulation times or effort, which would imply a captive nutritional deficiency. Work on feather-pecking in laying hens, a morphologically similar behaviour albeit directed at flock mates rather than self-directed (reviewed by van Zeeland et al., 2009; Mellor et al., 2018a), provides a logical starting point. Dietary supplementation of insoluble fibre (e.g. Aerni et al., 2000) and tryptophan (e.g. Savory, 1998; Savory et al., 1999; van Hierden et al., 2004) can reduce feather-pecking. Feeding extra insoluble fibre likely increases satiation, and thus reducing feather-pecking (e.g. van Krimpen et al., 2005; van

Krimpen et al., 2009). The biological relevance of tryptophan, is that it is a precursor for serotonin: an important neurotransmitter in the neural pathways responsible for modulation of behaviour (Garner, 2006), with SB associated with disruption of this system (Lewis et al., 2006; Novak et al., 2006). Both insoluble fibre and tryptophan are relevant to parrots: wild parrots consume 'debris' of no apparent nutritional value likely high in insoluble fibre (e.g. bark and pine needles: Kartal and Ozturk, 2016; Waliszewska et al., 2019), which may serve some digestive functionality (Gilardi and Toft, 2012; Martens et al., 2013; Toft, 2015); and tryptophan-rich foods include nuts, seeds and animal protein (e.g. estimated from human food: GOV.UK, 2019), i.e. some of the food items included in the calculation of FDB's biological risk factor identified here (see Section 4.2.2).

If my FDB result does reflect nutrient deficiency, then this uniquely predicts that supplying the missing nutrient should reduce or abolish FDB. Additionally, if feathers supply the missing nutrient or approximate its function (e.g. consumed feathers and fibre in hens, sensu: Harlander-Matauschek et al., 2006) then i) parrots should eat the feathers that that chew/pluck; and ii) species who experience the biggest deficit (i.e. their wild diets contain high levels of the missing nutrient) should spend the most time performing FDB/eat the most feathers (fibre suggestion based on pers. comm., with G. Mason [2020]), It is also plausible that a deficiency, e.g. as one might predict from a tryptophan deficiency, in the captive diet may cause changes in brain function (G. Mason, pers. comm., 2020), rendering affected animals more compulsive and/or perseverative (cf. Mason and Latham, 2004) – inappropriate repetitions of an ineffective response (Norman and Shallice, 1986; Garner, 2006). In this case, alleviating FDB by providing the missing nutrient would likely be much harder, if not impossible (sensu Mason and Latham, 2004), depending on the length of time the deficit was experienced for, i.e. the extent of the altered brain function. However, a logical prediction of this scenario is that affected individuals should show altered behaviour overall, e.g. be highly perseverative, and show difficulties in reacting to novel stimuli and environmental change (Mason and Latham, 2004).

4.4.2 Other SB results

In agreement with McDonald Kinkaid (2015) I did not find oral SBs to be predicted by wild foraging behaviour. This result is especially interesting because of similarities between oral SBs and FDB – both involve the beak, and both have been sensibly hypothesised elsewhere to relate to frustrated foraging behaviour (Keiper, 1969; Meehan et al., 2003b; Meehan et al., 2004; van Zeeland et al., 2009). I do note, though, that of the different forms of other SB, oral SB prevalence did correlate the most with FDB, albeit with a low R^2 value (=0.089; see Table 4.6). Likewise, FDB prevalence did also significantly correlate with oral SB, but weakly compared with the other forms of SB (R^2=0.127 v head-only SB model's R^2=0.425; see Table 4.6). My results indicate, though, that non-FDB forms of oral SB relate more to forms of whole-body SB, sharing a biological risk factor (relative brain volumes, cf. McDonald Kinkaid, 2015), and correlating more strongly with them than FDB. This seems to be in contrast to SBs of carnivores, as the annual home range size effect seems to relate specifically to route-tracing (including other forms of SB to route-tracing's severity weakens the annual home range size effect: Bandeli, 2018). In laying hens, Dixon et al. (2008) found that severe and gentle feather pecks also likely have different motivational bases: the morphology of severe feather pecks, but not gentle ones, was most similar to foraging pecks indicating the motivational basis of the former. While observing parrots performing FDB is rare (Meehan et al., 2003b), when they are seen chewing/eating feathers, they reportedly pick the rachis apart seemingly to eat the pulp (Y. van Zeeland, pers. comm., 2016) – plausibly similar to the way in which they would naturally de-husk seeds and nuts prior to consuming the pulp (cf. Ullrey et al., 1991; Koutsos et al., 2001). Therefore, perhaps when food-handling oral behaviours are thwarted in captivity, this *only* leads to development of SBs morphologically similar to the behaviour being restricted (this may be applicable to other taxa; see Section 7.3). For parrots, then, this could be why, despite similarities, it is FDB and *not* other oral abnormal behaviours that relates to natural foraging.

I also did not find route-tracing to be linked with restricted ranging associated with food search. Food search is just one of many aspects of ranging behaviour, e.g. primary productivity, population density, other resources such as nesting sites are further examples

(e.g. Clutton-Brock and Harvey, 1977b; McLoughlin and Ferguson, 2000; Rolando, 2002; Broomhall et al., 2003). Therefore, even if there were a relationship between restricted ranging and route-tracing, my predictor variable here might not be an adequate proxy for ranging in general. Ranging is a recognised biological risk factor for route-tracing across Carnivora (see Chapters 2 and 3; Clubb and Mason, 2003; Clubb and Mason, 2007; Kroshko et al., 2016; with a similar trend reported in; Miller et al., 2018) and Primates (Pomerantz et al., 2013). Therefore, even though my data do not support this hypothesis, I recommend re-visiting it at later stage with more appropriate predictor variable data (e.g. home range sizes and daily travel distances as used in the Carnivora and Primate studies; and/or proxies for flight ranging ability such as the hand-wing index, e.g. Baldwin et al., 2010; Claramunt et al., 2012; Weeks and Claramunt, 2014; Pigot and Tobias, 2015; Kennedy et al., 2016; Claramunt and Wright, 2017; Stoddard et al., 2017; Sheard et al., 2020).

4.4.3 Inter-relationships among forms of SB

Regarding the second and third aims of this chapter, my results examining inter-relationships between different types of whole-body SBs, oral SBs and FDB are in good agreement with Garner et al. (2006a), who similarly found FDB to be distinct from other SBs. Thus, in their epidemiological study FDB had higher heritability than other SBs, and had different risk factors: FDB was more severe in females, and progressively more severe the closer to the door birds were caged; whereas birds with fewer neighbours performed more other SBs (Garner et al., 2006a). Additionally, neither of my wild foraging predictors explained any of the variance in other SBs not explained by relative brain volumes, which further emphasises differences between FDB and other SBs. Overall, my results and those of Garner et al. (2006a), imply that FDB and other forms of SB are distinct behaviours.

Unlike studies of mink (Polanco et al., 2017; Polanco et al., 2018), my results support the suggestion that diverse forms of whole-body and oral SBs in parrots may be considered related responses to the challenge of captivity (i.e. that associated with large relative brain volumes) (McDonald Kinkaid, 2015). As summarised by McDonald Kinkaid (2015), they could

represent different ways of addressing problems associated with being relatively intelligent, such as having limited opportunities to explore, problem-solve and learn, or "boredom" in a monotonous captive environment. I do add the caveat that by noting of the whole-body SBs, route-tracing does appear least related to the others (Table 4.6), being the only one not to significantly correlate with the other subtypes though it *does* significantly correlate with oral SB prevalence. Therefore, while the most parsimonious approach in handling these data is, as I have, to pool them into a single 'all other SB' measure, I cannot rule out that some other unmeasured aspect of species-typical biology might explain route-tracing alone (ranging behaviour being the logical starting point, cf. Clubb and Mason, 2003; Clubb and Mason, 2007; Pomerantz et al., 2013; Kroshko et al., 2016; Miller et al., 2018). If so, an alternative explanation for the correlation between route-tracing and oral SBs is that, like the weak correlations between FDB and other SB subtypes (see Table 4.6), some species have more than one aspect of species-typical biology which when restricted affects their welfare, and that these multiple aspects covary. I would therefore recommend future researchers use caution and take care to investigate how different forms of SB relate, or not, to one another prior to pooling behaviours during analyses.

4.4.4 Recommendations for pet owners and the pet trade

Based on the biological risk factor identified here, I can make the following practical recommendations to help address FDB. For species reliant on wild food requiring extensive oral manipulation (see values in Table 4.2), I recommend feeding naturalistic diets by including the types of wild food (or a suitable domesticated equivalent) such species consume, such as shell-on tree nuts and invertebrates (the latter could be concealed in an enrichment device requiring the bird to use its beak to gain access). This recommendation circumvents the problem that, currently, the casual explanation for *why* reliance on these types of food results in FDB is unknown (see Section 4.4.1). That is, regardless of whether it is differences in food handling times or some nutritional deficiency that leads to FDB, this recommendation is appropriate for both. If owners have concerns over possible weight-gain due to increased nut consumption (as they have relatively high fat content: Ullrey et al., 1991), then it may be appropriate to reduce the proportion of pellets fed. Further to this, I

would recommend that manufacturers of commercial pelleted diets incorporate findings from here and from Rozek et al. (2010); Rozek and Millam (2011), and consider increasing the size of the pellets they produce to encourage increased handling times. Should future experimental research confirm that FDB relates a nutritional deficiency in captive diets (Section 4.4.1), then diet formulation should be adjusted accordingly.

Experimental works have demonstrated that foraging enrichments extend foraging times of captive parrots (Rozek et al., 2010; van Zeeland et al., 2013), and can reduce the effects of FDB (i.e. result in improved feather condition) (Lumeij and Hommers, 2008). More generally, foraging enrichments are readily used and valued by captive animals, often improving welfare (e.g. Markowitz and LaForse, 1987; Forthman et al., 1992; Shepherdson et al., 1993). Therefore, I encourage owners to provide such environments to their birds, especially foraging enrichments designed to encourage oral manipulation to access food items, e.g. hiding food in cardboard boxes or using puzzle feeders, including providing plentiful appropriate chewing substrates (see Section 4.4.1). It should be noted that if FDB is associated with altered brain function (see Section 4.4.1) then introducing new enrichment devices or making other changes should be gently done, as such animals might initially find these changes difficult (Mason and Latham, 2004).

Regarding the pet trade, I recommend that species with the biological risk factor identified here, as being inherently less suitable as pets. Examples from my dataset include Solomons cockatoos (FDB: 67%), salmon-crested cockatoos (52%), yellow-collared macaws, *Primolius auricollis* (50%), and red-shouldered macaws *Diopsittaca nobilis* (40%). Further examples of such species *not* included in my dataset include: yellow-tailed black cockatoos, *Calyptorhynchus funereus*, glossy black cockatoos, *C. lathami*, dusky parrots, *Pionus fuscus*, blue-winged macaws, *Primolius maracana*, and thick-billed parrots, *Rhynchopsitta pachyrhyncha* (all have a relative reliance of ≥80% on wild food requiring extensive oral manipulation; see Appendix 5). This because their natural foraging behaviour, or dietary needs, are so hard to cater for under current captive dietary conditions that a sign of poor welfare, FDB, is more likely to be prevalent. Examining Figure 4.3 and Table 4.2 it is also

evident that some species are affected by both prevalent FDB and SB, some already mentioned, e.g. Solomons cockatoo (67% FDB; 50% SB) and red-shouldered macaws (40% FDB; 30% SB), and others, e.g. Tanimbar cockatoo, *Cacatua goffiniana* (53% FDB; 40% SB), yellow-crested cockatoo (33% FDB; 44% SB). From a welfare perspective, these species are obvious targets for intensive species-specific work aimed at addressing their welfare problems, and one must also ask whether these particular species are really suitable as pets.

4.5 Conclusions

In this chapter I uncovered a biological risk factor for feather-damaging behaviour in parrots: being reliant on a wild diet requiring extensive oral manipulation (i.e. relatively long food handling times). Despite sharing similarities with FDB, conversely, wild foraging behaviour did not predict oral SBs, nor did it predict route-tracing. As assumed here, FDB could result from the mismatch in oral manipulation required between wild and captive diets, but an alternative explanation is that nutritional differences between the two are instead the driver. These hypotheses should now be addressed experimentally. Based on the risk factor identified here, practical recommendations to address this specific welfare-relevant management problem relate to increasing the handling time and effort required to access food items, e.g. naturalistic diets such as shell-on tree nuts, and enrichment devices such as puzzle feeders and chewing substrates. For the pet trade, species with this biological risk factor are less suitable as pets as their foraging behavioural needs, or dietary requirements, are so much harder to meet in captivity. Regarding the secondary aim of this chapter, while FDB is distinct from other forms of abnormal behaviour, other forms of SB are inter-related and may represent related responses to captivity's challenges. Finally, my approach here highlights a few species who should be targets for intensive species-specific work aimed at addressing their welfare problems, as their populations have such prevalent behavioural problems. Should these issues prove difficult to resolve, their continued use in the pet trade must be questioned.

Chapter 5: An ecological approach to understanding susceptibility to weight gain in captive lemurs

Abstract

Excessive body weight, i.e. being overweight or obese, is concerning in captive animals being associated with fat-levels that may impair health, and problems such as reduced fertility and lifespan. Some lemur species are prone to extreme weight gain and potential obesity in captivity, yet for others a healthy body condition is typical. Understanding the basis for species differences in susceptibility to weight gain in captivity, is fundamental to address the problem and improve captive health and welfare. Madagascar, to which all lemurs are native, is characterised by poor plant productivity and unpredictable inter-year climatic variation, both of which affect food resource availability. Adaptations to these environmental conditions may result in some species being especially "thrifty" (storing fat when food is available) and thus prone to weight gain under well-provisioned captive conditions. Wild lemurs also vary in arboreality, which increases the mass-dependent costs of locomotion, and could explain why some species consistently maintain lower fat levels. Alternatively, wild predation risk might be the driver, as excess weight impedes escape. Using phylogenetic generalised least squares regressions to control for species' non-independence, I explored relationships between proxies for species-typical food resources within the native range (annual rainfall; inter-year annual rainfall coefficient of variation), arboreality (frequency of ground use; relative tail length), and predation risk (predation score), and my outcome: species-typical median 'relative body mass' (calculated as the deviation from wild-type body mass). Weight records and data on corresponding living conditions were collected using a survey, yielding useable data on 675 adult animals representing 13 species from 96 collections worldwide. Data on species-typical wild ecology

were collated from published literature and online climate databases. I found tentative support for one hypothesis: species that experience large inter-year variation in annual rainfall, and thus greater food resource unpredictability, tend to have larger species-typical relative body masses. Based on this I discuss priority species for research attention, because their body masses deviate the most from their wild norms; make practical recommendations to address unwanted captive weight gain; and highlight that relative body mass as a proxy for body condition requires validation, along with some appropriate methods of achieving this.

5.1 Introduction

Excessive body weight, i.e. being overweight or obese, is a health concern being associated with fat-levels that may impair health (WHO, 2019). In humans, a weight-for-height (kg/m^2) 'body mass index' is typically used to classify these conditions (≥ 25 being overweight, and ≥30 obese: WHO, 2019), and a similar index also used for some non-human primates (e.g. Nunamaker et al., 2012); as is skinfold thickness (e.g. Videan et al., 2007); waist circumference measurements (the upper 20^{th} percentile of the population's range the typical threshold for obesity) (e.g. Schmitt et al., 2018); and visual body condition scoring systems (e.g. Clingerman and Summers, 2005; Summers et al., 2012; Millette et al., 2015). Body weight is also an acceptable indicator of body fat: those weighing 20-25% over the ideal are considered obese, and more likely to have comorbidities of obesity (e.g. in humans, dogs, *Canis lupus familaris*, and cats, *Felis catus*: Kealy et al., 2002; Selassie and Sinha, 2011; Laflamme, 2012). Serious health problems comorbid with being overweight or obese include metabolic syndrome, diabetes, heart disease, impaired reproduction, orthopaedic disorders, and cancers across humans and non-human animals (Kopelman, 2000; Hatt and Clauss, 2006; Bauer et al., 2011; Laflamme, 2012; Vaughan and Mattison, 2016; RSPCA, 2019). Positive energy imbalance, i.e. calorific intake greater than expenditure, is central to weight gain (Trayhurn, 1984; Selassie and Sinha, 2011). Energy balance is affected by environmental, e.g. diet and physical activity levels, and genetic factors (Selassie and Sinha, 2011), e.g. obesity is heritable (e.g. vervet monkeys, *Chlorocebus pygerythrus*, despite being on a low calorie diet: Kavanagh et al., 2007), and obesity-risk varies between human populations (Asayama et al., 2003), breeds of companion (Giles et al., 2014; RSPCA, 2019) and farm animals, and strains of laboratory animals (Trayhurn, 1984).

Lemuriformes ("lemurs") are a Primate infraorder native only to the island of Madagascar. All extant lemurs originate from one common ancestor (Yoder et al., 1996; McLain et al., 2012), indicating a single historical colonisation event by an ancestral species (but see Gunnell et al., 2018), likely a sea-crossing from mainland Africa (Mittermeier et al., 2010). Currently ~100 lemur species and five families are recognised, with many taxonomic

refinements made since the 1980s (McLain et al., 2012). Lemur species occupy various ecological niches, vary in size from the smallest known primates at 23-29cm (mouse lemurs, *Microcebus* spp.) to the indris, *Indri* spp., at 64-72cm (Mittermeier et al., 2010), and until recently provided the only known examples of hibernation in a primate (see Ruf et al., 2015). Wild lemurs face threats such as habitat loss (estimated at up to 90%: Schwitzer et al., 2013), hunting, and harvesting for the pet market (Mittermeier et al., 2010), exacerbated by ongoing economic and political issues on the island. Indeed, over 96% of the 95 species assessed for the International Union for Conservation of Nature's Red List, are 'Near Threatened' or above (IUCN, 2019), making lemurs some of the most threatened species on the planet (Schwitzer et al., 2013).

In captivity, lemur species vary in susceptibility to weight gain. For instance, ring-tailed lemurs, *Lemur catta*, and blue-eyed black lemurs, *Eulemur flavifrons*, are prone to weight gain, yet a healthy body condition is typical of greater bamboo, *Prolemur simus*, and red-bellied lemurs, *E. rubriventer* (Terranova and Coffman, 1997; Taylor et al., 2012). Across some captive populations, problems such as obesity can be prevalent, e.g. using a weight-based definition of obesity (two standard deviations from the wild mean weight) 46.5% black-and-white ruffed and red ruffed lemurs, *Varecia variegata* and *V. rubra*, housed in European zoos were deemed obese (Schwitzer and Kaumanns, 2001). Of 902 zoo lemurs from 14 species, again using a weight-based method to infer body condition, 54% were classified as being overweight or obese (two and four or more standard deviations from species-typical wild mean weights: Taylor et al., 2012). Given the associations between excessive weight and other health problems outlined in the opening paragraph, such prevalent high body masses is concerning, especially for a taxonomic group as threatened as lemurs (cf. Schwitzer et al., 2013). Obesity in particular may affect conservation breeding programmes because it hinders reproduction, and obese animals are considered unsuitable for reintroduction into the wild (Schwitzer and Kaumanns, 2009). Therefore, understanding the basis for the excessive body masses observed in some species is fundamental to address this management problem, improve health and welfare, and promote conservation.

Next, I introduce and discuss four aspects of species-typical biology that might explain the observed species differences in susceptibility to weight gain in captive lemurs. Two relate to "thriftiness" associated with adaptations to Madagascar's environment and food resource availability, one to arboreality, and the fourth to predation pressure.

Primates have evolved "thrifty" physiological adaptations to store fat during times of plenty (Shively et al., 2009), to buffer against future resource-restriction (i.e. "thrifty genotypes" sensu: Neel, 1962), and lemurs are no exception. Madagascar's harsh environment, which affects food resource availability, has resulted in lemurs evolving ways to conserve energy and maximise use of scarce resources (Pereira, 1993; Wright, 1999). Regarding thriftiness, there are two potential explanations for the observed species differences in captive weight gain. The first relates to a potential mismatch between wild and captive food resources (sensu Section 1.1). Madagascar's soil quality and plant productivity are poor relative to other countries' forests at equivalent latitudes or bearing other similarities (e.g. number of tree and primate species), and this varies across the island (Wright, 1999). Central, west, and northern regions have especially long dry seasons, and the south receives very little annual rainfall; whereas eastern areas often receive relatively high rainfall year-round (Tattersall and Sussman, 1975; Ganzhorn et al., 2001; Mandl et al., 2018). Total annual rainfall is commonly used in the primate literature to infer primary productivity (Bronikowski and Altmann, 1996; Ossi and Kamilar, 2006; Gordon et al., 2016), because it directly affects plant growth (Rosenzweig, 1968; Yan et al., 2015) and thus food availability. Therefore, while all lemur species are adapted to existing with relatively poor food resources, some species likely experience poorer resources than others. Wild food quality contrasts with that provided in captivity (Hosey et al., 2013c) – a mismatch cited in the excessive body masses observed in some captive lemurs (Schwitzer and Kaumanns, 2001; Goodchild and Schwitzer, 2008; Junge et al., 2009). Commercial fruits especially are far higher in energy and sugar content than wild equivalents (Goodchild and Schwitzer, 2008; Junge et al., 2009). A similar mismatch has been proposed to explain why some domestic horse breeds, *Equus caballus*, are prone to obesity and its related health problems (Frank et al., 2010) in the well-provisioned companion animal setting, (i.e. they are similarly physiologically adapted to low quality foodstuffs: Giles et al., 2014). Therefore, for some

species their thrifty adaptations to low productivity and poor food resources, as experienced within their natural environments, might result in excessive weight gain in captivity.

The second thrifty explanation for susceptibility to captive weight gain, relates to adaptations to cope with unpredictability in wild food resource availability. Madagascar experiences severe droughts and cyclones, the frequency and severity of which varies across the island and between years, as well as El Niño events (Wright, 1999). Food resources can be restricted or even totally wiped out because of these severe weather events (Wright, 1999; Godfrey et al., 2004; Pavelka and Behie, 2005; Lewis and Rakotondranaivo, 2011). As a result, lemur populations in affected areas can decline, suffer increased mortality, reduced fecundity (Wright, 1999; Ratsimbazafy, 2002; Godfrey et al., 2004; Dunham et al., 2011), and loss of body condition (Fardi et al., 2018). However, this is not always true (e.g. Erhart and Overdorff, 2008; Johnson et al., 2011; Lewis and Rakotondranaivo, 2011) and it appears that some species have evolved adaptations to manage unpredictable environmentally challenging events. Diet switching, reduced activity levels (Ratsimbazafy, 2002), temporary reductions or even cessation of reproduction (Godfrey et al., 2004), seem to facilitate coping with environmental stress. Total annual rainfall, a proxy for primary productivity and food resource availability as mentioned above (Gordon et al., 2016), in the north and south of Madagascar especially varies between years; hypothesised to explain unpredictability of fruit availability (Dewar and Richard, 2007). Indeed, tree species may unpredictably flower and fruit on irregular, extended, asynchronous, or alternate year cycles (Wright, 1999). In other species, resource unpredictability is associated with maintenance of larger fat stores, to protect against scarcity (Rogers, 1987; Ekman and Hake, 1990; Rogers, 2015). It follows, then, that these thrifty adaptations to resource unpredictability within the wild environment, might render the same species prone to weight gain in the reliably well-provisioned captive environment.

I now detail the third aspect of species-typical biology that might explain species variation in captive weight gain: arboreality. Wild lemurs vary in how readily they use the ground. Ring-

tailed lemurs, for instance, are deemed 'semi-terrestrial' (Mittermeier et al., 2008). Aye-ayes, *Daubentonia madagascariensis*, also frequent ground-level, reportedly second only to ring-tailed lemurs in their ground-use (Mittermeier et al., 2010). Grey mouse, *Microcebus murinus*, lemurs hunt and even occasionally nest on the ground (Lutermann et al., 2010). However, many other species are arboreal specialists, preferring the canopy, e.g. ruffed lemurs (Garbutt, 2007), and only come to ground if absolutely required, e.g. to drink (Scholz and Kappeler, 2004) or to retrieve fallen young (Vasey et al., 2018). Across mammals, including lemurs, terrestrial species carry higher fat stores than do arboreal ones (Heldstab et al., 2016). Arboreality imposes limits on how much body fat arboreal primates can develop, because of the energetic costs and restrictions on agility associated with carrying excess fat tissue (Dittus, 2013; Heldstab et al., 2016). Therefore, being naturally arboreal could be *protective* against weight gain in captivity, because of upper limitations on body fat stores associated with an arboreal lifestyle.

Finally, predation risk could explain the observed species differences in susceptibility to weight gain. Increased predation pressure is associated with relatively smaller fat stores in birds, reptiles and mammals, because carrying excess weight impedes escape (Houston et al., 1993; Witter and Cuthill, 1993; Witter et al., 1994; Kullberg et al., 1996; Higginson et al., 2012; Zamora-Camacho et al., 2014; Speakman, 2018). To the best of my knowledge, direct evidence for such patterns in lemurs is non-existent. However, lifespan in wild grey mouse lemurs was negatively correlated with body mass, which the authors suggest could result from selective predation on the heavier individuals (Hämäläinen et al., 2014). Based mainly on these theoretical works and empirical evidence from birds, then, high wild predation risk could explain why some species consistently maintain smaller fat stores, even when in captivity.

The aim of this chapter is to test the following four hypotheses, with their corresponding predictions, regarding ecological explanations for species differences in susceptibility to weight gain in captive lemurs:

i. Susceptibility to weight gain in captivity relates to physiological adaptations to low productivity within the native range on Madagascar.
   → *Prediction*: species whose geographic ranges are least productive should be relatively heavier in captivity.
ii. Susceptibility to weight gain in captivity relates to physiological adaptations to unpredictable food resource availability within the native range.
   → *Prediction*: species whose geographic ranges are most variable should be relatively heavier in captivity.
iii. Susceptibility to weight gain in captivity relates to species-typical arboreality.
   → *Prediction*: the least arboreal species should be relatively heavier in captivity.
iv. Susceptibility to weight gain in captivity relates to species-typical predation risk.
   → *Prediction*: the least predated species should be relatively heavier in captivity.

5.2 Methods

5.2.1 Outcome variable

My outcome variable was species-typical median 'relative body mass'. As detailed in the Introduction (Section 5.1), there are several ways to determine body condition in primates, e.g. body mass index (e.g. Nunamaker et al., 2012), skinfold thickness (e.g. Videan et al., 2007), waist circumference measurements (e.g. Schmitt et al., 2018), and visual body condition scoring systems are available for some primates (e.g. Clingerman and Summers, 2005; Summers et al., 2012) including one for ring-tailed lemurs (Millette et al., 2015). However, most of these at minimum require direct access to animals, some are relatively invasive, and applicability across the sexes may vary (e.g. Videan et al., 2007). Additionally, none of these methods to-date have been tested and validated for use in lemurs. For lemurs, published values of species-typical mean wild adult weights are readily available (Taylor and Schwitzer, 2011), and comparisons between these and captive animals' body masses have been used elsewhere to infer body condition across several lemur species by Taylor et al. (2012). This weight-based method of inferring body condition comes with

several advantages. Zoos routinely keep many records of their animals, such as body masses (Hosey et al., 2013a). Such records are highly useful for studies such as mine and, unlike the other methods described at the start of this section, require no direct contact with animals. Furthermore, zoo records from round the world can be cheaply and effectively gathered electronically, thus yielding valuably generalisable future results (see also Section 2.4.3). I acknowledge that this method is limited in that it does not account for frame (unlike, for example, body mass index); however, such frame measurements are rarely readily available.

Calculation of relative body mass is based upon Taylor and colleagues (2012)'s work. For each species, a predicted 'healthy' body mass range was first defined, this being up to two standard deviations from the wild. Species-typical wild means were calculated by Taylor and Schwitzer (2011), and collated via literature searches; means being calculated as they were the statistic most commonly reported in the literature. When averaged over all species, this yielded a threshold of 25% above and below the wild means. Based on this, by calculating the percentage of an adult captive animal's body mass relative to its species-typical wild mean, Taylor et al. (2012) categorised 902 individuals from 14 species as being healthy, overweight, obese or morbidly obese (75-125%, >125%, >150%, and >200% of species-typical wild mean weight respectively).

For my purpose here, I calculated relative body mass in almost exactly the same way as Taylor et al. (2012), albeit calculated as the ratio between a captive animal's body mass and its species-typical wild mean. Note that for my analyses, the continuous relative body mass values were my outcome variable, and I provide the corresponding body condition thresholds (cf. Taylor et al., 2012) for illustrative purposes only:

- → Underweight: values of <0.75 represent the captive animal being less than 75% of its wild average
- → Healthy: values of 0.75-1.25 correspond with an animal being 75 – 125% of its wild average
- → Overweight: values of 1.25-1.5 means the animal is 125-150% of its wild average

→ Obese: values of 1.5-2 and the animal would be 150-200% of its wild average

→ Morbidly obese: values of 2 or more mean the animal is twice the size (or more) of its wild average

5.2.1.1 Outcome variable data collection

I collected data on captive lemurs' body masses using a survey (see Appendix 6 for a list of the questions). Participants could either provide values within the survey itself, or they could provide Zoological Information Systems (ZIMS) Specimen Reports for their lemurs which, if recorded, include body mass records. Environment and living conditions also contribute to weight gain (Selassie and Sinha, 2011) and, should these covary with my wild biology predictors, could be confounds (see Section 2.4.4; and after: Clubb and Mason, 2003; Clubb and Mason, 2007; Kroshko et al., 2016). Therefore, my survey also collected information on lemurs' living conditions so that I could statistically control for these effects where necessary. Most collections made responses in an online version of the survey created using Google Forms, suitable for collections with up to 10 enclosures. Larger collections (>10 enclosures) completed a tailored Excel spreadsheet containing the same questions. On my request, the Duke Lemur Center (www.lemur.duke.edu) kindly provided detailed copies of their most recent records of body masses (an update of: Zehr et al., 2014), housing, and feeding and enrichment routines of their lemurs, which I incorporated into my dataset.

To increase the likely response rate, I requested support from the British and Irish Association of Zoos and Aquariums (BIAZA) Research Committee; the European Association of Zoos and Aquaria Prosimian Taxon Advisory Group (TAG); the Association of Zoos and Aquariums (AZA, North America) Prosimian TAG; and the Zoo and Aquarium Association (ZAA, Australasia) Primate TAG. My BIAZA and AZA Prosimian TAG applications were successful, and their letters of support were circulated with my participation requests to zoos. Likewise, ZAA Primate TAG also stated their support to their members.

Requests to participate in my study were emailed to Species360 collections worldwide (see Appendix 7). I targeted zoos with lemurs by requesting 'species holding' information from Species360 (then, the International Species Information System): members of the public can request this information for up to five species, once per month (Species360, 2012). With the assistance of a summer student, Shelley Jackman, I used this information to create a mailing list. After initial contact, up to two further reminder emails were sent. Zoos were classed as non-participatory if no response was received after the third email, or if the zoo declined to participate. The survey was live and collecting responses from August 2016 – January 2018.

5.2.1.2 Outcome variable data processing

The raw online survey data were extracted from Google Forms, and entered into an Excel spreadsheet along with responses from the larger zoos providing data in other formats (see Section 5.2.1.1). This raw dataset had records from 1,386 animals from 22 species from 133 collections worldwide. With the assistance of two undergraduate students, Georgia Dacombe and Rachel Brown, I processed the raw survey responses into quantitative, species-level variables, combining responses from some questions. For most lemurs, ZIMS Specimen Reports were provided. I used dates of birth and weighing to calculate age at most recent weighing. Seasonal variation in body masses does occur across some species in the wild (e.g. Lewis and Kappeler, 2005; Simmen and Rasamimanana, 2018), but because most species had values from two or more seasons I assumed any seasonal effects would be represented within my sample. Lemurs have a late 'near-adult' growth period, in which animals are sexually mature but not yet fully grown (Zehr et al., 2014). To ensure that such animals did not artificially lower my species summary statistics (i.e. my final outcome variable) downwards, after Zehr et al. (2014) I excluded records from all but adult animals (I classed 'adults' ≥ twice the minimum dam age of reproduction, as defined by Zehr et al. (2014) for lemurs housed at the Duke Lemur Center; see Table 5.1 for these). For the minority of animals without ZIMS Specimen Reports, I accepted the respondents' judgement of 'adult'. This could have resulted in not yet fully-grown young adults entering the species summary statistic but, importantly, would not unduly skew my results upward. As I was interested in species, any hybrid animals were excluded. I also excluded adults missing body mass values, those of unknown sex, and pregnant females. After these exclusions I was left

with records, including some on living conditions, for 756 animals from 22 species (see Appendix 8 for species-typical median relative body masses for these). Using their most recent body mass value, I calculated each animal's species-specific relative body mass as described in Section 5.2.1.

Species with natural programmed fattening

Two of my 22 species, fat-tailed dwarf lemurs, *Cheirogaleus medius*, and grey mouse lemurs, undergo seasonal hibernation or torpor during Madagascar's dry season. Prior to this individuals naturally undergo programmed fattening (sensu Dark, 2005) and can rapidly gain weight, e.g. fat-tailed dwarf lemurs can double their body masses in weeks, which they later lose during their inactive period (Fietz and Ganzhorn, 1999; Fietz and Dausmann, 2007). This temporary fat storage, unlike conditions like obesity, is not pathological (Trayhurn, 1984). Because these species demonstrate such pronounced seasonal fluctuations in wild weight (Ortmann et al., 1997; Atsalis, 1999; Fietz and Ganzhorn, 1999; Giroud et al., 2008; but see: Randrianambinina et al., 2003), I was interested whether captive animals also show a similar pattern. For 21/22 and 44/52 adult fat-tailed dwarf lemurs and grey mouse lemurs respectively, their weight records provided were detailed enough for me to track their body mass fluctuations over an entire year. For each species in turn, for individuals with complete records I first calculated mean monthly body masses, then from these individual means plotted species-typical body masses (with standard deviations) over an entire year (see Appendix 9). Like their wild counterparts, a similar seasonal pattern of weight gain and loss was evident in these captive animals too (although living in the northern rather than southern hemisphere, opposite to that of their wild counterparts). For most of the captive representatives of these species their most recent body masses (as recorded for my outcome calculation for all other species) were taken during autumn only, when they would likely be at their largest. Therefore, I could not be confident that seasonality effects would be adequately captured in my samples of these species. Because of differences in their biology relating to natural fat storage compared to the other 20 species in the dataset, and because seasonality was unlikely to be represented in their captive samples I excluded fat-tailed dwarf lemurs and grey mouse lemurs from my analyses. Note that a preferred

alternative to exclusion could have been to deal with the biological difference statistically, as an additional term in subsequent models ('torpor/hibernation': yes *versus* no') as a control. However, just two species use these strategies which does not meet the N≥5 species per level for categorical predictors (see Chapter 3; Bandeli et al., in prep.). After these species were excluded, my dataset included records for 691 animals from 20 species.

To ensure representativeness, I next excluded species represented by fewer than five adult animals (after Kroshko et al., 2016; McDonald Kinkaid et al., in prep.). Note that because for many species I did not have ≥5 animals per sex, I was unable to consider sex differences in my analyses (obesity and its related effects do differ between the sexes across primates: Power and Schulkin, 2008; Ely et al., 2013; Obanda et al., 2014). My final dataset featured 675 animals representing 13 species held across 96 collections worldwide. For each species in turn, I then calculated a median across individuals' relative body masses to yield my outcome variable: *species-typical median relative body mass*. Note: although Taylor and Schwitzer (2011) reported sub-species body masses for the *Varecia* sub-species, as my analyses were of species I pooled their relative body mass values for the species summary statistic calculation (though for individual relative body mass calculations I used the sub-species wild weight appropriate to each in my dataset [*Varecia varigata subcincta and V. v. variegata*]).

Table 5.1 Ages (in days) from which each species is considered adult (see Section 5.2.1.2 for rationale). Values are rounded to the nearest whole number.

Species name	Common name	Dam minimum age at conception (years)	Adult from: (days)*
Daubentonia madagascariensis	Aye-aye	4.22	3,081
Eulemur collaris	Red-collared lemur	1.64	1,197
Eulemur coronatus	Crowned lemur	1.71	1,248
Eulemur flavifrons	Blue-eyed black lemur	1.59	1,161
Eulemur fulvus	Common brown lemur	1.39	1,015
Eulemur macaco	Black lemur	1.48	1,080
Eulemur mongoz	Mongoose lemur	1.78	1,299
Eulemur rubriventer	Red-bellied lemur	1.78	1,299
Hapalemur alaotrensis *(H. griseus)*	Alaotran gentle lemur	1.53	1,117
Lemur catta	Ring-tailed lemur	1.34	978
Propithecus coquereli	Coquerel's sifaka	2.64	1,927
Varecia rubra	Red ruffed lemur	1.67	1,219
Varecia variegata	Black-and-white ruffed lemur	1.61	1,175

* Twice the minimum dam age at conception (following: Zehr et al., 2014)

NB: As the Duke Lemur Center only holds one of the black-and-white ruffed lemur sub-species, and the sub-species are considered very similar, I used this (1,175 days) as the cut off for both sub-species in my dataset. One species in my dataset, Alaotran gentle lemur, *Hapalemur alaotrensis,* is not held by the Duke Lemur Center. I therefore used values from its closest relative, *Hapalemur griseus* (1,117 days), as indicated in parentheses.

5.2.1.3 Husbandry confound data processing

I also processed data on the following aspects of the environment believed a priori to affect body condition and weight gain. Hormonal contraceptives are associated with weight gain in primates (Portugal and Asa, 1995), including lemurs (Terranova and Coffman, 1997), and surgical castration can induce obesity in other taxa (Trayhurn, 1984). Enclosure area was used to infer quality of usable space. I assumed that smaller values represent fewer exercise opportunities and less physical activity, and an increased likelihood of weight gain (sensu Selassie and Sinha, 2011). Being primates and adapted to use a three-dimensional space, enclosure volume would perhaps be the preferred metric; however, this was reported far less frequently in my survey and was unusable. Similarly, fixed climbing structures were assumed to require less physical effort to climb than flexible ones, and a less enriched environment was assumed to represent fewer exercise/activity opportunities, which could both contribute to weight gain (sensu Selassie and Sinha, 2011). Commercial, domesticated fruit are more energy-rich than the fruits wild lemurs consume, and thus a higher proportion of fruit in the captive diet could also lead to weight gain (Goodchild and Schwitzer, 2008). I thus calculated these as species-typical husbandry variables to be used as statistical controls in hypothesis-testing models (see Table 5.2 and Table 5.3 for methods and species' values).

Ethical approval for data collection was granted by the Faculty of Health Sciences Research Ethics Committee of the University of Bristol (University Investigation Number: 37201).

Table 5.2 Details of lemur survey data processing (see Sections 5.2.1.2 and 5.2.1.3).

Individual-level information	Definition	Levels or type	Species-level variable	Details
Relative body mass	For adults only, the ratio of the most recent weight recorded (grams): its species-typical wild mean (grams)	Continuous	Median relative body mass	Median calculated across all adult animals
Enclosure area	Total area (m^2) of the enclosure*	Continuous	Median enclosure area	Median calculated across enclosures
Enrichment score	Types of enrichment scored according to their provision: daily (5), two/three times per week (4), weekly (3), monthly (2), less than monthly (1), never (0). Summed across for a maximum total score of 25 *Enrichment types:* Foraging-related, manipulable, olfactory, audio/visual, and training	Continuous	Median enrichment score	Median calculated across enclosures
Dietary fruit	Proportion of the diet fed that is fruit	Continuous	Median proportion of fruit in the diet	Median calculated across enclosures

Individual-level information	**Definition**	**Levels or type**	**Species-level variable**	**Details**
Climbing structures	Type of climbing structures within the enclosure(s)** *Fixed:* climbing structures that are rigid and fixed into place, e.g. platforms, bolted down logs *Flexible:* climbing structures that are unstable and flexible e.g. ropes, branches on a living tree	Flexible Fixed	Proportion with flexible climbing structures	Proportion of enclosures with flexible climbing structures
Contraceptive status	Is the lemur given contraception/neutered?	Yes No Unknown	Proportion given contraception	Proportion of animals given contraception, of the animals whose contraceptive status is known

*Summed across indoor and outdoor enclosures

**For animals with both indoor and outdoor enclosures, if one had flexible climbing structures but the other did not they were recorded as 'flexible'

5.2.2 Predictor variable data collation

From published literature, for my 13 species with outcome data I collated data on the following six predictor variables to test my hypotheses (see Table 5.3 for species' values):

i. Low productivity hypothesis predictor

a. Annual rainfall

As mentioned in Section 5.1, total annual rainfall is commonly used in the primate literature because it directly affects plant growth (Rosenzweig, 1968; Yan et al., 2015) and thus food availability. WorldClim's (version 2) website www.worldclim.org/version2 provides global values averaged across 1970-2000 for several bioclimatic variables at 1km^2 spatial resolution, including annual total rainfall (Fick and Hijmans, 2017). For each species in turn, using its native geographic range as detailed in its IUCN Red List's species' account (IUCN, 2019), I extracted the mean annual total rainfall within each using QGIS (version: Maderia 3.4) (QGIS Development 2019a). For some species, ranges are fragmented rather than being one continuous area. For these, a median was calculated across their range fragments' values (I also did this for my second climate predictor variable, described next).

Data were available for 13 species. If my data support this hypothesis, I expect species from ranges with low annual rainfall to have larger species-typical relative body masses.

ii. Unpredictable food resources hypothesis predictors

a. Inter-year annual rainfall coefficient of variation

0.5^o x 0.5^o gridded global monthly values for total rainfall between 1901-2016 came from the Climate Research Unit, University of East Anglia (CRU version 4.01) (Harris et al., 2014). For each species in turn, I calculated the mean total rainfall that fell each month during this time period within its geographic range in R (version 3.6.1: R Core Team 2019) using the packages 'maptools' (Bivand et al., 2019b), 'raster' (Hijmans et al., 2019) and 'rgdal' (Bivand et al., 2019a). Then, I summed monthly values within each year, yielding annual values for total rainfall. Next, to capture between-year unpredictability I calculated the coefficient of variation of these annual total rainfall values:

$$\mathrm{CV} = \frac{\sigma}{\mu} \times 100$$

Where σ is the standard deviation of the annual total rainfall values, and μ is the mean of these values. Larger values indicate more inter-year variation and thus unpredictability in annual rainfall and, therefore, food resource availability. My assumption here is that environments variable on a between-year scale, are also more variable at the shorter time periods most relevant to relatively small-bodied primates such as lemurs (i.e. days and weeks). While climate data on a daily or weekly scale might have been the preferred predictor, I have not encountered such data in the literature, necessitating the use of the scale (between-year) I have used here.

Data were available for 13 species. If my data support this hypothesis, I expect species with large rainfall coefficient of variation values to have larger species-typical relative body masses.

iii. Arboreality hypothesis predictors

a. Ground use (common v rare)

For this variable I used species' use of the ground as a proxy for degree of adaptation to arboreality, i.e. those that come to ground the most I assumed were *least* arboreal. Data for this variable were collated via a systematic literature search in Web of Science, using species' scientific and common names as search terms (as detailed in the first two columns of Table 5.1). Additionally, I used the same terms to search for relevant theses in the British Library's EThOS Thesis Repository (EThOS, 2017). Studies were included if they were of native, free-living wild-born populations. Unlike in Chapter 3, I did not impose a minimum study period for inclusion; many field studies were relatively short, and this would have resulted in severe data loss. As many studies presented information and summary statistics of groups, including juveniles, I likewise did not impose an adults-only criterion (see Chapter 3). Finally, I also gleaned information from two field-guides and a textbook (Garbutt, 2007; Macdonald, 2009; Mittermeier et al., 2010).

I used two methods to categorise each species' ground use as 'common' or 'rare'. Firstly, I used descriptive terms from field studies and field-guides. Terms such as 'often' or 'sometimes', and reports of the species regularly foraging, travelling and/or nesting at ground-level categorised a species as 'common'. Conversely, terms such as 'rarely' and 'almost never' categorised a species as 'rare'. If sources disagreed, I used the most frequently occurring classification as its species-typical ground use category (in practise, this rarely occurred). Secondly, I incorporated behavioural data on ground use (see b) % scans at ground level), and classed species that typically spent ≥10% scans at ground-level as 'common'. This is an arbitrary threshold, but in all but one case it showed good agreement with the descriptive terms method just mentioned. The one instance of disagreement was for crowned lemurs, *Eulemur coronatus.* Here, because the field study providing the behavioural data was only 4 months long, I judged the field-guides' reports to be more reliable, and thus classed this species as 'common' category despite reportedly only spending 1% of scans at ground-level.

Data were available for 11 species. If my data support this hypothesis, I expect species that commonly come to ground to have larger species-typical relative body masses.

b. Ground time (% scans)

As mentioned, my systematic literature searches yielded behavioural data on time spent on the ground (% scans). For species with values from >1 study, I calculated the median value across studies.

Data were available for eight species. If my data support this hypothesis, I expect species that typically spend more time on the ground to have larger species-typical relative body masses.

c. Relative tail length

This is the tail length as a proportion of the entire length of the animal, from head to tail tip. Larger values correspond to relatively longer tails: an adaptation to arboreality across

primates (Schmidt, 2011; Gebo, 2014; Sehner et al., 2018). Data on tail and head-tail lengths came from two field-guides: Garbutt (2007) and Mittermeier et al. (2010).

Data were available for 13 species. If my data support this hypothesis, I expect species with relatively short tails to have larger species-typical relative body masses.

v) Predation risk hypothesis predictor

a. Predation score (0-3)

The ideal predictor for this hypothesis would be some measure of direct predation pressure, e.g. typical number of species predated by; number of predation attempts per 24hr. However, during the literature searches I made for hypothesis iii), it became apparent that such detailed data are not available for the majority of species. However, broad taxonomic descriptions of species (e.g. 'raptors') a lemur species is typically predated by are reported in the two field-guides already mentioned (Garbutt, 2007; Mittermeier et al., 2010). I assumed that being predated by different classes of species (relevant here: mammals, birds, reptiles) likely represents necessity for different predator-avoidance strategies by lemurs. Evolving different anti-predator behaviour across classes likely represents a greater investment than pressure to evolve it for just one, and so may indirectly correspond with species-typical predation pressure.

I calculated predation pressure as follows. For each lemur species in turn, I scored the number of classes of native predator reported in Mittermeier et al. (2010) and Garbutt (2007), as a maximum of 1 each for reported mammalian, avian, and/or reptilian predation, and summed across these for a maximum total score of 3. If one source provided greater detail than the other, I used the more detailed one in my calculation.

Data were available for 13 species. If my data support this hypothesis, I expect species with low predation scores to have larger species-typical relative body masses.

5.2.3 Confound checks

Prior to hypothesis-testing, I performed two checks. First, I investigated potential correlations between predictor variables belonging to different hypotheses. Based on these, I made further checks during hypothesis-testing to ensure that interpretation of a focal predictor was not explained by a correlated predictor, by including the latter as an extra term. Correlated predictors were included in final hypothesis-testing models only if their inclusion significantly affected the result (in practice, this never occurred).

My outcome is also affected by living conditions (Selassie and Sinha, 2011) and, should these systematically vary with my wild biology predictors (sensu Section 2.4.4), could be a source of confound. Therefore, I also assessed relationships between my wild biology predictor variables and the five aspects of species-typical husbandry mentioned above (Section 5.2.1.3). Correlated husbandry variable(s) were included in final hypothesis-testing models.

5.2.4 Statistical analyses

Statistical procedures were the same as per Chapter 3, with the following differences. For my predictor and husbandry confound checks, I used a consensus phylogenetic tree (Figure 5.3), freely available from: www.10ktrees.nunn-lab.org (Arnold et al., 2010). When ground use was analysed as an outcome during between-predictor checks, I used phylogenetic logistic regression models in the 'phylolm' package (Ho and Ané, 2014). To account for phylogenetic uncertainty (see Section 2.4.6), all my final hypothesis-testing models were performed over a tree block of the 1,000 alternative lemur phylogenetic trees from the same source (Arnold et al., 2010), and results from these models are reported as medians and 95% CIs (shown in square parentheses).

5.3 Results

5.3.1 Descriptive statistics

Of 359 zoos contacted 135 responded, representing a response rate of 38%. Of my 13 species, their sample sizes and species-typical relative body masses are shown in Table 5.3 and Figure 5.1 provides a visual depiction of several ring-tailed lemurs across three conditions (healthy, overweight and obese; I did not have photographs of animals in underweight or morbidly obese conditions.

Figure 5.2 displays boxplots of individuals' relative body masses, grouped by species. Across my final dataset, 0.30% of animals were underweight (species-typical relative body mass <0.75), 57.63% were healthy (0.75-1.25), 28.30% were overweight (1.25-1.5), 13.33% were obese (1.5-2) and 0.44% were morbidly obese (>2). Species-typical median relative body mass values of eight species corresponded with the healthy category: aye-ayes, red-collared lemur, *E. collaris*, mongoose lemurs, *E. mongoz*, red-bellied lemurs, Alaotran gentle lemurs, *Hapalemur alaotrensis*, Coquerel's sifaka, *Propithecus coquereli*, and black-and-white and red-ruffed lemurs. Four species were classed as being typically overweight: crowned lemurs, blue-eyed black lemurs, black lemurs, *E. macaco*, and ring-tailed lemurs. One species, common brown lemur, *E. fulvus*, was classed as being obese.

Figure 5.3 shows the phylogenetic tree of my 13 species, with their corresponding species-typical median relative body mass value as coloured tip-points.

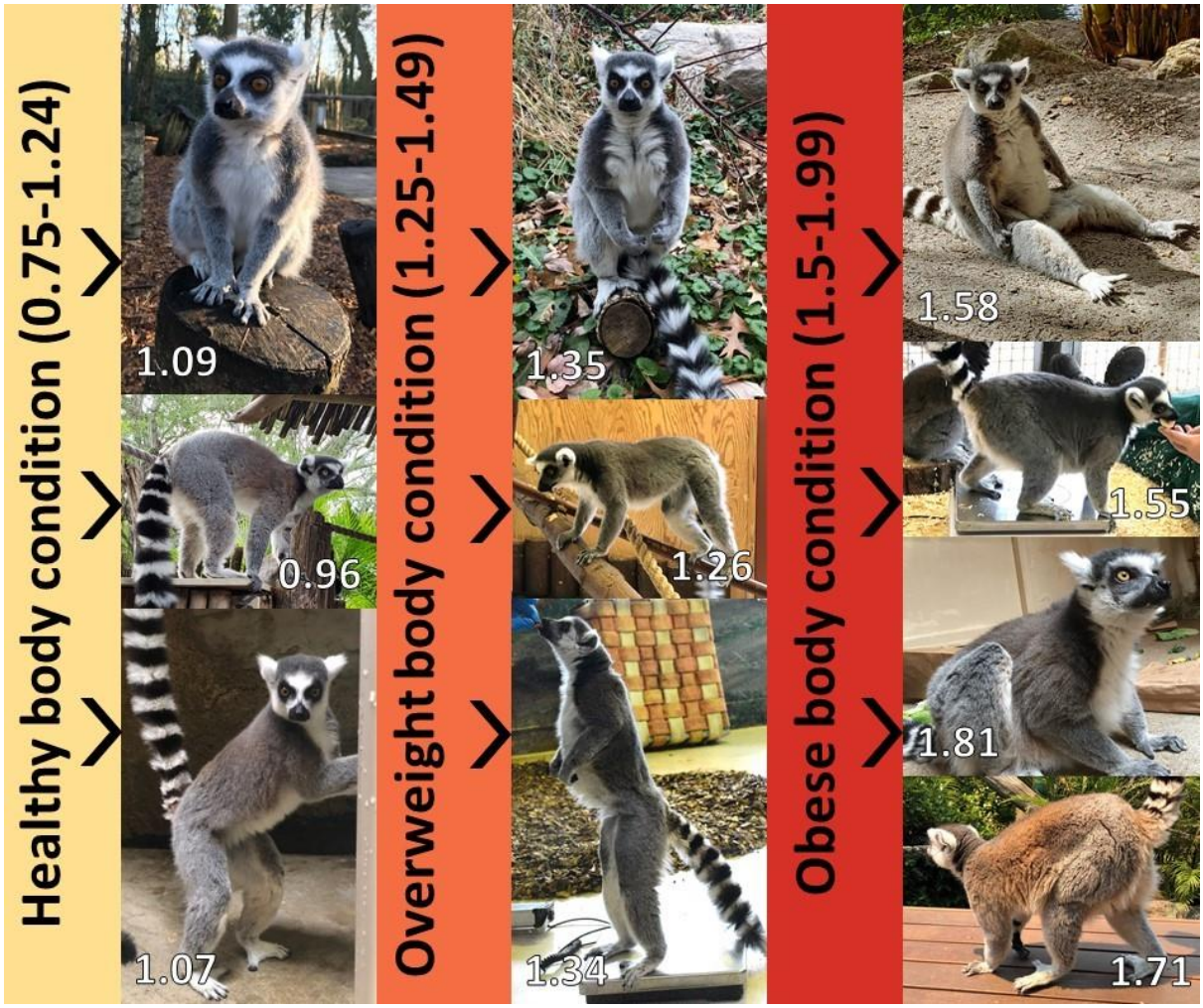

Figure 5.1 Images of different adult ring-tailed lemurs in one of three conditions: healthy, overweight, or obese (note I did not have images of lemurs classed as underweight or morbidly obese). The number at the bottom of each image is that animal's relative body mass at the time the photograph was taken. Sex of lemurs (credits). Far left, top: female (Lakeland Wildlife Oasis); middle: male (Nancy Nill, Palm Beach Zoo); bottom: female (Ashley Ashcraft). Middle, top: male (Valerie Schultz, Smithsonian's National Zoo); middle: female (Śląski Ogród Zoologiczny); bottom: male (Heidi Beal). Right, top: male (Nancy Nill, Palm Beach Zoo); second from top: female (Śląski Ogród Zoologiczny); second from bottom: male (Debbie Fenton); bottom: male (Rebecca Lambert, Taronga Conservation Society).

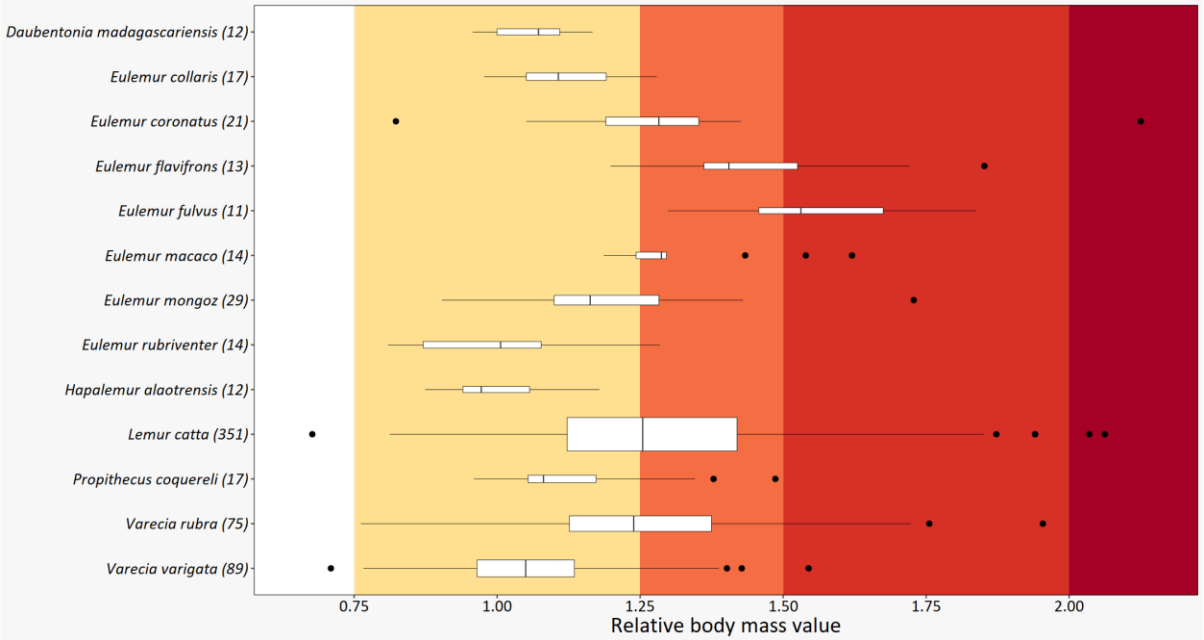

Figure 5.2 Box-and-whisker plots of relative body mass values of individual adult lemurs, grouped by species. Sample sizes are shown in parenthesis next to species' names, and are also are indicated by the relative width of their respective boxplot. Species' medians are indicated by notches on the boxplots; the extent of the boxes indicate their interquartile ranges; whiskers represent values within 1.5 times the interquartile range; and outliers outside this are depicted as points. The healthy range (0.75-1.25) is shown by yellow shading; overweight by orange (1.25-1.5); obese by red (1.5-2); and morbidly obese (>2) by the darker red.

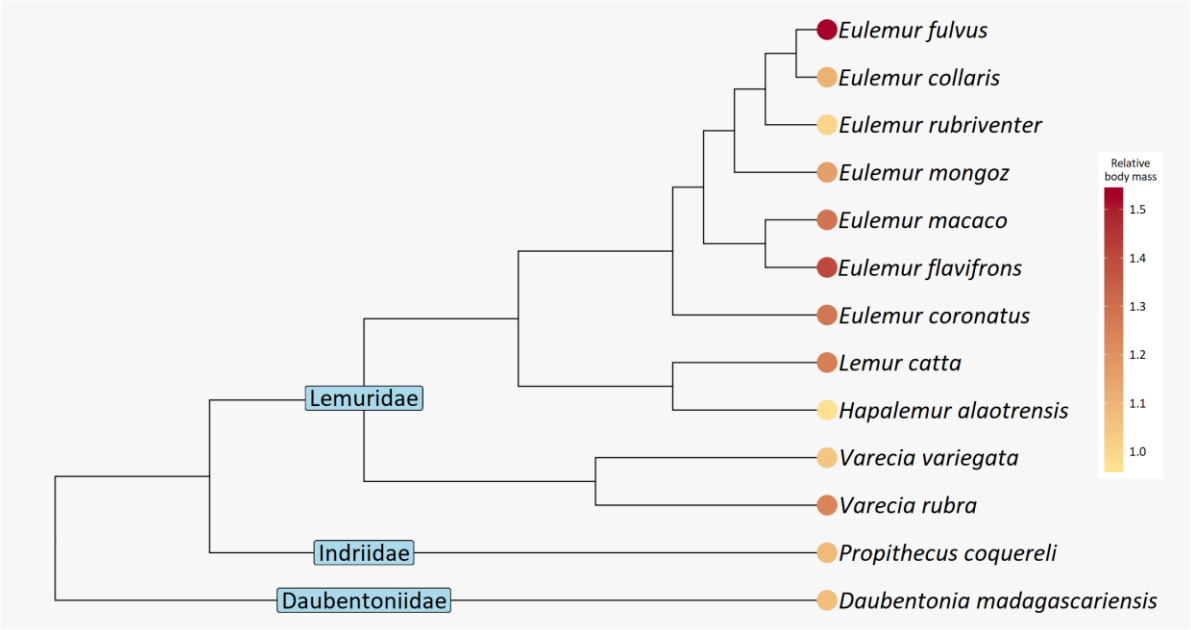

Figure 5.3 Phylogenetic tree of 13 lemur species in my analyses, with their species-typical median relative body mass values shown as tip-points. The colour of a species' point represents its species-typical body condition: the healthy range (species-typical relative body mass 0.75-1.25) is shown by yellow shading; overweight by orange (1.25-1.5); obese by red (1.5-2); and morbidly obese (>2) by the darker red.

Table 5.3 Lemur comparative dataset used for analyses. Note that acronyms are explained at the foot of the table. Rationale and justification for all variables are described in Sections 5.2.1 and 5.2.2. Dashes indicate data were not available for that species.

		Species-typical outcome			Species-typical wild biology						Species-typical husbandry			
Species name	**Common name**	**RBM**	**N**	**SD**	**AR**	**ARCV**	**GU**	**GT**	**RTL**	**PS**	**MEA**	**MEE**	**MPF**	**PFC**	**PGC**
Daubentonia madagascariensis	Aye-aye	1.07	12	0.07	2472.25	16.05	Common	-	0.59	0	26.13	14	0.13	0.9	0
Eulemur collaris	Red-collared lemur	1.11	17	0.09	1445.59	19.59	Rare	2.5	0.57	2	38.05	18	0.29	1	0.15
Eulemur coronatus	Crowned lemur	1.28	21	0.24	1438.58	26.0	Common	1	0.56	2	72	15	0.24	1	0
Eulemur flavifrons	Blue-eyed black lemur	1.41	13	0.19	1706.97	19.86	Rare	0.6	0.61	2	49.10	14	0.29	0.89	0
Eulemur fulvus	Common brown lemur	1.53	11	0.16	1482.72	14.27	-	-	0.46	2	12.95	18	0.25	0.86	0.45
Eulemur macaco	Black lemur	1.29	14	0.13	1961.93	23.78	Rare	0.58	0.58	2	72.59	14.5	0.05	1	0.5
Eulemur mongoz	Mongoose lemur	1.16	29	0.17	1481.21	15.60	Rare	1	0.59	2	36	18	0.33	1	0.14

		Species-typical outcome			Species-typical wild biology						Species-typical husbandry			
Species name	**Common name**	**RBM**	**N**	**SD**	**AR**	**ARCV**	**GU**	**GT**	**RTL**	**PS**	**MEA**	**MEE**	**MPF**	**PFC**	**PGC**
Eulemur rubriventer	Red-bellied lemur	1.01	14	0.15	1718.98	14.55	Rare	-	0.56	2	102.25	13.5	0.29	0.83	0
Hapalemur alaotrensis	Alaotran gentle lemur	0.97	12	0.09	1151.84	14.20	Common	-	0.50	2	20	17	0	1	0.08
Lemur catta	Ring-tailed lemur	1.25	351	0.24	701.205	20.03	Common	27	0.58	3	142.91	14	0.27	0.90	0.33
Propithecus coquereli	Coquerel's sifaka	1.08	17	0.14	1527.47	17.23	Common	-	0.54	0	14188.39	14	0.01	1	-
Varecia rubra	Red ruffed lemur	1.24	75	0.22	2873.58	20.56	Rare	0.01	0.57	0	227.60	14	0.40	0.93	0.19
Varecia variegata	Black-and white ruffed lemur	1.05	89	0.15	1869.95	16.75	Rare	1.1	0.54	0	144.79	14	0.29	0.97	0.12

Acronyms:

Outcome variable: **RBM**: species-typical median relative body mass*;* **N**: number of individuals with outcome data*;* **SD**: standard deviation of species-typical median relative body mass.

Species-typical wild biology predictor variables: **AR**: annual rainfall (mm)*;* **ARCV**: inter-year rainfall coefficient of variance*;* **GU**: ground use (common v rare)*;* **GT**: ground time (% scans)*;* **RTL**: relative tail length (proportion of tail length to whole body length)*;* **PS**: predation score (0-3).

Species-typical husbandry variables: **MEA**: median enclosure area; **MEE:** median enrichment score; **MPF**: median proportion of the captive diet that is fruit; **PFC**: proportion of enclosures with flexible climbing materials; **PGC**: proportion of captive animals known to be given contraception.

5.3.2 Results of confound checks

Results of all between-predictor confound checks are shown in Table 5.4. The following aspects of species-typical wild biology were found to significantly relate to one another:

Species that spend more time on the ground live in ranges with low annual rainfall (t_6=-3.641, N=8, R^2=0.688, λ=0.505, P=0.011), and vice versa (t_6=-9.308, N=8, R^2=0.935, λ=0, P<0.001). Species more heavily predated also live in ranges with low annual rainfall (t_{11}=-3.164, N=13, R^2=0.476, λ=0.771, P=0.009).

Results of predictor-husbandry checks are shown in Table 5.5. None of my wild biology predictor variables significantly related to the five species-typical husbandry variables.

Table 5.4 Results of models investigating potential relationships among predictor variables belonging to different hypotheses. PGLS models were used for continuous outcomes, and phylogenetic logistic regression was used to analyse ground use as an outcome. CV = coefficient of variation. Dashes indicate that the analysis could not be performed (because neither PGLS nor phylogenetic logistic regression models are appropriate for ordinal outcome variables like predation risk). Results were considered significant at P<0.05, and trends (P<0.01) are italicised. All P values are two-tailed.

Hypothesis:	*iii) low productivity*	*ii) unpredictability*		*iv) arboreality*		*v) predation risk*
Outcome: **Predictor:**	**Annual rainfall (mm)**	**Inter-year rainfall CV**	**Ground use (rare v some)**	**Ground time (% scans)**	**Relative tail length***	**Predation score (0-3)**
Annual rainfall (mm)		t_{11}=0.252, N=13, R^2=0.006, λ=0, P=0.806	Z=-1.245, N=12, α=0.0430, P=0.213	**t_6=-9.308, N=8, R^2=0.935, λ=0, P<0.001**	t_{11}=0.340, N=13, R^2=0.010, λ=0, P=0.741	-
Inter-year rainfall CV	t_{11}=0.400, N=13, R^2=0.014, λ=0.902, P=0.697		Z=0.037, N=12, α=0.077, P=0.970	t_6=-0.226, N=8, R^2=0.008, λ=0, P=0.829	t_{10}=1.110, N=12, R^2=0.110, λ=0, P=0.293[a]	-
Ground use (rare v some)	t_{10}=-1.662, N=12, R^2=0.217, λ=0.652, P=0.127	t_{10}=0.019, N=12, R^2<0.001, λ=0, P=0.985				-

Hypothesis:	*iii) low productivity*	*ii) unpredictability*		*iv) arboreality*		*v) predation risk*
Outcome: **Predictor:**	**Annual rainfall (mm)**	**Inter-year rainfall CV**	**Ground use (rare v some)**	**Ground time (% scans)**	**Relative tail length***	**Predation score (0-3)**
Ground time (% scans)	**t_6=-3.641, N=8, R^2=0.688, λ=0.505, P=0.011**	t_6=-0.226, N=8, R^2=0.008, λ=0, P=0.829				-
Relative tail length*	t_{11}=0.292, N=13, R^2=0.008, λ=0.908, P=0.776	t_{10}=1.465, N=12, R^2=0.177, λ=0, P=0.174[a]				-
Predation score (0-3)	**t_{11}=-3.164, N=13, R^2=0.476, λ=0.771, P=0.009**	t_{11}=0.523, N=13, R^2=0.024, λ=0, P=0.612	Z<0.001, N=12, α=0.104, P=0.9997	*t_{16}=2.193, N=8, R^2=0.445, λ=0, P=0.071*	t_{11}=-0.005, N=13, R^2<0.001, λ=0, P=0.996	

* This is the length of the tail as a proportion of the entire length of the animal, from head to tail tip.

Outlier removed: [a]*Eulemur fulvus*

Table 5.5 Results of PGLS models investigating potential relationship between species-typical husbandry and wild biology predictor variables. In all models the husbandry variables are outcome variables. Dashes indicate an analysis could not be performed due to too few species per level for ground use (see Section 5.2.4). CV=coefficient of variation. Results were considered significant at P<0.05, and trends (P<0.01) are italicised. All P values are two-tailed.

Hypothesis:	Wild biology predictor	Median enclosure area (m^2)	Median enrichment score (0-25)	Median proportion of diet fruit	Proportion given contraception	Proportion with flexible climbing materials
i) low productivity	**Total annual rainfall (mm)**	t_{11}=0.228, N=13, R^2=0.005, λ=0.001, P=0.824	t_{11}=-1.273, N=13, R^2=0.128, λ=0, P=0.229	t_{11}=0.676, N=13, R^2=0.040, λ=0, P=0.513	t_{10}=-0.605, N=12, R^2=0.035, λ=0, P=0.559	t_{11}=-0.318, N=13, R^2=0.009, λ=0, P=0.756
ii) unpredictability	**Inter-year rainfall CV**	t_{11}=1.643, N=13, R^2=0.197, λ=1, P=0.129	t_{11}<0.001, N=13, R^2=0.076, λ=0, P=0.362	t_{11}=0.261, N=13, R^2=0.006, λ=0, P=0.799	t_{10}=0.393, N=12, R^2=0.015, λ=0, P=0.703	t_{11}=1.265, N=13, R^2=0.127, λ=0, P=0.232
iii) arboreality	**Ground use (some v rare)**	t_{10}=0.352, N=12, R^2=0.012, λ=1, P=0.732	t_{10}=-0.337, N=12, R^2=0.011, λ=0, P=0.743**	*t_{10}=-2.155, N=12, R^2=0.317, λ=0, P=0.057*	-	t_{10}=0.327, N=12, R^2=0.011, λ=0, P=0.751

Hypothesis:	Wild biology predictor	Median enclosure area (m^2)	Median enrichment score (0-25)	Median proportion of diet fruit	Proportion given contraception	Proportion with flexible climbing materials
	Ground time (% scans)	t_6=0.352, N=8, R^2=0.012, λ=1, P=0.732	t_6=0.461, N=8, R^2=0.034, λ=0, P=0.661	t_6=-1.046, N=8, R^2=0.154, λ=0.060, P=0.336	t_6=0.255, N=8, R^2=0.011, λ=0, P=0.808	t_6=-0.008, N=8, R^2<0.001, λ=0, P=0.994
	Relative tail length*	t_{11}=-0.458, N=13, R^2=0.019, λ=0, P=0.656	t_{11}=-1.638, N=13, R^2=0.196, λ=0, P=0.130	t_{11}=0.275, N=13, R^2=0.007, λ=0, P=0.789	t_{10}=-1.270, N=12, R^2=0.139, λ=0, P=0.233	t_{11}=-0.280, N=13, R^2=0.007, λ=0, P=0.785
iv) predation risk	**Predation score (0-3)**	t_{11}=-0.468, N=13, R^2=0.019, λ=0, P=0.656	t_{11}=1.363, N=13, R^2=0.145, λ=0, P=0.200	t_{11}=0.265, N=13, R^2=0.006, λ=0, P=0.796	t_{10}=0.653, N=12, R^2=0.041, λ=0, P=0.528	t_{11}=-0.259, N=13, R^2=0.006, λ=0, P=0.800

* This is the proportion of the length of the tail compared to the entire length of the animal, from head to tail tip.

** Note that the residuals from this model did not pass a Shapiro-Wilks normality test, despite numerous transformation attempts, so this result should be treated cautiously.

5.3.3 Hypothesis-testing results

No aspect of wild biology was found to significantly predict species-typical median relative body mass (Table 5.6). However, as shown in Table 5.6 and Figure 5.4 species that experience large between-year variation in rainfall, and thus greater food resource unpredictability, tend to have larger species-typical relative body masses (as the 95% CI values are identical [see Table 5.6], here I report median values for each parameter: t_{11}=2.039, N=13, R^2=0.274, λ<0.001, P=0.066).

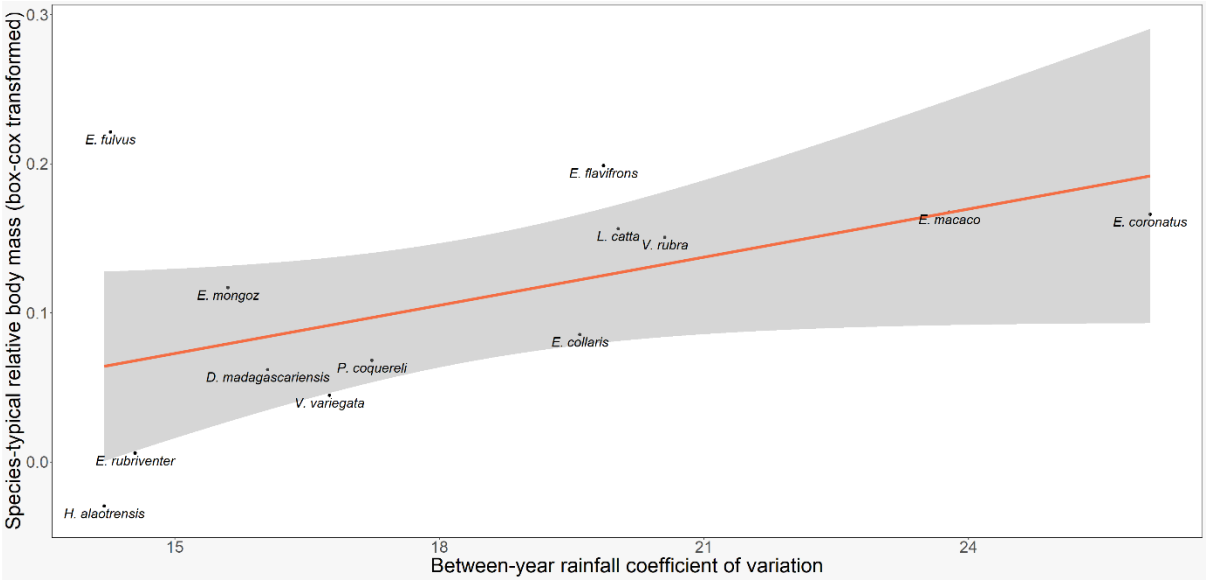

Figure 5.4 Relationship between between-year rainfall coefficient of variation and species-typical median relative body mass across 13 lemur species (each species' datapoint is labelled, with genus abbreviated to the first letter). Species that experience large between-year variation in rainfall, and thus greater resource unpredictability, tend to have larger relative body masses (t_{11}=2.039, N=13, R^2=0.274, λ<0.001, P=0.066). The shaded area shows the 95% confidence region.

Table 5.6 Results of hypothesis-testing model results performed over a tree block of 1,000 alternative Lemuriform phylogenetic trees. Here, results are summarised as the median value for each parameter followed by its 95% confidence intervals (CIs) in square parentheses. CV=coefficient of variation. Results were considered significant at P<0.05, and trends (P<0.01) are italicised. All P values are two-tailed.

Hypothesis	Wild biology predictor	Model output [95% CIs]
i) low productivity	**Total annual rainfall (mm)**	t_{11}=-0.098 [-0.098, -0.098], N=13, R^2=0.001 [0.001, 0.001], λ<0.001 [<0.001, <0.001], P=0.924 [0.924, 0.924]
ii) unpredictability	**Inter-year rainfall CV**	*t_{11}=2.039 [2.039, 2.039], N=13, R^2=0.274 [0.274, 0.274], λ<0.001 [<0.001, <0.001], P=0.066 [0.066, 0.066]*
iii) arboreality	**Ground use (some v rare)**	t_{10}=-0.585 [-0.585, -0.585], N=12, R^2=0.033 [0.033, 0.033], λ<0.001 [<0.001, <0.001], P=0.572 [0.572, 0.572]
	Ground time (% scans)	t_6=-0.314 [-0.314, -0.314], N=8, R^2=0.016 [0.016, 0.016], λ<0.001 [<0.001, <0.001], P=0.764 [0.764, 0.764]
	Relative tail length*	t_{11}=-0.145 [-0.145, -0.145], N=13, R^2=0.002 [0.002, 0.002], λ<0.001

Hypothesis	Wild biology predictor	Model output [95% CIs]
		[<0.001, <0.001], P=0.887 [0.887, 0.887]
iv) predation risk	**Predation score (0-3)**	t_{11}=1.177 [1.177, 1.177], N=13, R^2=0.112 [0.112, 0.112], λ<0.001 [<0.001, <0.001], P=0.264 [0.264, 0.264]

*This is the proportion of the length of the tail compared to the entire length of the animal, from head to tail tip.

5.4 Discussion

In this study, I found no clear support for my hypotheses relating susceptibility to captive weight gain to low productivity, to arboreality, or to predation risk. However, given the sample sizes of my analyses were small which likely reduced power to detect effects (N<20; cf. Blomberg et al., 2003), it is worth discussing the trend that supported one hypothesis. Lemurs whose native ranges have variable between-year annual rainfall, and who are thus adapted to environments with unpredictable food resource availability, tended to have larger relative body masses in captivity. Thus, such "thrifty" adaptations may be a biological risk factor for excessive weight gain in captivity, pre-disposing such species to potential obesity and its related health problems.

Across my 13 species, 42% of individuals were classed as overweight or heavier: over 10% less than the 54% reported by Taylor et al. (2012)'s study of 14 species. Notably, my study had more overweight (28% v 21%) but fewer morbidly obese animals (0.44% v 21%) than in Taylor et al. (2012), perhaps indicating that some steps have already been taken to address unwanted weight gain in captive lemurs.

My study has some good between-species agreement with Taylor et al. (2012) and another similar multi-species study by Terranova and Coffman (1997) on species-typical body

condition of captive lemurs (summarised in Table 5.7). In two out of the three instances of disagreement, species-typical body conditions may have improved: mongoose lemurs and red-ruffed lemurs are typically healthy in my study but were overweight in previous ones. Mongoose lemurs were also overweight nearing obesity (average weight 1,862g; relative body mass=1.46) in a survey by Schaaf and Stuart (1983). Red-ruffed lemurs in European zoos were also typically overweight (mean weight ~4,250g; relative body mass=1.41), and black-and-white ruffed lemurs near overweight (mean weight ~4,500g; relative body mass=1.28) (estimated from Figure 3 in: Schwitzer and Kaumanns, 2001). These between-study differences could just reflect differences in data sources and measurement method used, or they might represent improvements in suitable captive diet design and husbandry (e.g. based on recommendations in: Goodchild and Schwitzer, 2008). What is striking in Table 5.7 are the consistencies in typical body condition across these three studies, both for healthy species such as red-bellied and Alaotran gentle lemurs and, more worryingly, for those typically overweight such as ring-tailed, blue-eyed black and black lemurs. Therefore, research efforts should now be aimed toward examining weight gain and potential obesity in the species whose typical body conditions are consistently large across studies, assessing how it affects animal health, and what the best strategy might be to address it (see Section 5.4.1 for recommendations).

Table 5.7 Table describing agreement (in bold) and differences (in italics) between this and two other multi-species studies of species-typical body condition of captive lemurs (Terranova and Coffman, 1997; Taylor et al., 2012). Dashes indicate a species was not featured in that study. Species-typical body condition based on relative body mass thresholds (after: Taylor et al., 2012), with species-typical relative body mass values in parentheses. Note: I calculated these for the other two studies myself from the values provided in the publications, and Terranova and Coffman (1997) reported species *means* in their study, rather than medians.

Species name	Common name	This study	Taylor et al. (2012)*	Terranova and Coffman (1997)
Daubentonia madagascariensis	Aye-aye	Healthy (1.07)	-	-
Eulemur collaris	Red-collared lemur	**Healthy (1.11)**	**Healthy (1.23)**	-
Eulemur coronatus	Crowned lemur	**Overweight (1.28)**	*Healthy (1.23)*	**Overweight (1.28)**
Eulemur flavifrons	Blue-eyed black lemur	**Overweight (1.41)**	**Overweight (1.48)**	**Overweight (1.27)**
Eulemur fulvus	Common brown lemur	Obese (1.53)	-	-
Eulemur macaco	Black lemur	**Overweight (1.29)**	**Overweight (1.49)**	**Overweight (1.25)**

Species name	Common name	This study	Taylor et al. (2012)*	Terranova and Coffman (1997)
Eulemur mongoz	Mongoose lemur	*Healthy (1.16)*	**Overweight (1.30)**	**Overweight (1.27)**
Eulemur rubriventer	Red-bellied lemur	**Healthy (1.01)**	**Healthy (1.05)**	**Healthy (1.04)**
Hapalemur alaotrensis	Alaotran gentle lemur	**Healthy (0.97)**	**Healthy (1.18)**	-
Lemur catta	Ring-tailed lemur	**Overweight (1.25)**	**Overweight (1.43)**	-
Propithecus coquereli	Coquerel's sifaka	Healthy (1.08)	-	-
Varecia rubra	Red ruffed lemur	*Healthy (1.24)*	*Overweight (1.35)*	-
Varecia varigata	Black-and white ruffed lemur	**Healthy (1.05)**	**Healthy (1.15)**	**Healthy (1.00)**

* Species-typical median relative body mass values are estimated from Taylor et al. (2012)'s graph, and provided here to give perspective.

Notable limitations of my study might include species (mis)identification. Lemur taxonomy is ever being updated, especially within the last 30 years (McLain et al., 2012). Therefore, I cannot rule out species mis-identification of some of the captive animals in my sample especially for *Eulemur* animals (Mittermeier et al., 2010), or too animals that contributed to the species-typical wild means (Taylor and Schwitzer, 2011). My study also has unequal representation of families (just one Indriiae and no Cheirogaleidae representatives, the latter for reasons given in Section 5.2.1.2), and a relatively small sample size, which limits generalisability and statistical power. Ideally, a minimum sample size of 20 species is required for acceptable power and Type I error rates (Blomberg et al., 2003). As mentioned in Section 5.2.1.2, I would have preferred to statistically control for species that use hibernation/torpor rather than excluding them, thus exacerbating loss of statistical power, but this was unavoidable. A larger sample size including more species using these strategies would enable this (Table 1 in Dausmann and Warnecke (2016) provides a list of such species). Sample sizes within species were also highly variable, ranging from 11 common brown lemurs up to 351 ring-tailed lemurs, which could affect accuracy of species-typical values (although my use of species medians rather than means should help mitigate this, sensu: Gittleman, 1989). Additionally, some of the species-typical wild means were calculated from reported values in studies taken at various times of year, i.e. representing seasonal variation, but not all. The wild means of red-collared lemurs (Donati et al., 2007) and Coquerel's sifaka (Andriantompohavana et al., 2006), for example, do not include seasonal variation, as each were calculated from weights taken when animals are likely at their leanest (at the end of the dry season/very start of the wet). My study thus requires replication including larger within- and between-species sample sizes of captive animals; ideally with updated wild mean body masses including seasonal variation across all species; and reflecting current understanding of taxonomic relationships, especially amongst *Eulemur* spp.

Interestingly, the better-sampled species in my dataset appear to have a greater range in relative body mass values (see Figure 5.2). This is especially clear for ring-tailed lemurs: the range of values for this species included healthy and obese animals, with outliers in the underweight and morbidly obese categories. Furthermore, the standard deviation of

species-typical relative body masses for ring-tailed lemurs is the largest, and a similar pattern is also observed for red-ruffed lemurs (see Table 5.3). Usually, higher sampling effort results in *smaller* variance in values, larger samples being more accurate and increasingly likely to include the true population mean (Field et al., 2012). There are two possible, and testable, explanations for this. Firstly, these ranges could reflect these species' greater potential for fat storage, whether pathological or not (see Section 5.4.2, pp. 197-198). Alternatively, within-species variability in body size, i.e. length and height rather than fatness, as anecdotally reported for different lineages of both ruffed species, might explain these patterns (C. Eddie, pers. comm., 2019). Relaxed selection pressure in captivity can lead to morphological change and increased attribute variability over generations (e.g. Kruska, 1996; Crossley and del Mar Miguélez, 2001; McPhee, 2004). Increased body size variability in captive populations have been reported for some (prawns, *Macrobrachium rosenbergii*: Peebles, 1979; cited in: Price, 1984), but not all species (wild vervet monkeys, *Chlorocebus pygerythrus*, varied more: Turner et al., 2016), and so is likely taxon-specific (Kamaluddin et al., 2019). Within-species variability in body size *not* linked with fatness is a topic I return to below.

Why might "thrifty" adaptations to unpredictable wild food resources potentially increase susceptibility to captive weight gain in lemurs? Lemurs have various attributes proposed to facilitate survival in their native, and unpredictable, environment. These include increased resting, food-switching (e.g. from fruit to leaves and flowers), reduced basal metabolic rates and hibernation/torpor during lean periods, as well as seasonal breeding, weaning synchrony, and female-dominance (Wright, 1999). Therefore, lemurs are most likely adapted to take advantage of plentiful food when it is available (cf. Wright, 1999) as, presumably, the captive environment is. Possibly, if captive food is delivered in one or two bouts (meals) rather than encountered slowly over the course of a day as per wild food, this could promote binge-eating. If captive food also tends to be energy-rich (a reasonable assumption) then my result might simply reflect a constant state of positive energy imbalance and subsequent weight gain (sensu Selassie and Sinha, 2011).

An alternative, more speculative, explanation relates to signalling of captive food (un)predictability. Across human populations, prevalence of overweight and obese people is highest in wealthier countries, and relates to socioeconomic position: people from lower positions are more likely to be overweight or obese than those from higher positions (especially so for women) (McLaren, 2007; Nettle et al., 2017). That people from wealthier countries have greater access to energy-rich foods than those from poorer countries does not adequately explain this relationship (Nettle et al., 2017). Instead, it seems the combination of food availability being perceived as insecure (i.e. unpredictable) at times, and when food-insecure people *can* access food is it is energy-rich, that explains this effect (Nettle et al., 2017). Experimental studies have shown that European starlings, *Sturnus vulgaris*, increase their body masses when food is unpredictably available (e.g. Cuthill et al., 2000; van Berkel et al., 2018). A similar effect could, plausibly, be relevant for the potential biological risk factor uncovered here. Thus, despite being reasonably assumed as reliably well-provisioned, if food is signalled as being unpredictable in some way then for animals from the "thriftier" species (see also Section 6.4) this could trigger adaptive behaviours and physiological mechanisms associated with coping during unpredictable times in the wild (e.g. increased resting, reduced basal metabolic rate: Wright, 1999). Even if provided at regular times each day, when effects of social hierarchy and feeding priority are factored in, food provided in a small number of discrete meals rather than being available *ad libitum* might in itself signal unpredictability (see also Sections 6.4 and 7.3). This may be especially the case for animals in which eating meals just two or three times per day is likely at odds – a mismatch – with their foraging and eating behaviour during times of plenty in the wild. In humans, attempts to lose weight via episodes of restrictive dieting are usually counterproductive, ultimately resulting in weight gain because such dieting likely cues food insecurity and triggering fat-storage mechanisms when food becomes available (Nesse, 1984; Williams and Nesse, 1991; Mann et al., 2007; Pietiläinen et al., 2012; Nettle et al., 2017). For captive lemurs, especially the "thrifty" ones, these adaptations combined with being provisioned with energy-rich food (cf. Goodchild and Schwitzer, 2008; Junge et al., 2009) in a small number of daily bouts could therefore result in weight gain. Somewhat counterintuitively then, giving animals access to *more* (low-calorie) not less food might therefore help address unwanted weight gain.

5.4.1 Recommendations for zoos

One of the great practical benefits of a comparative study is that identified risk factors inform tailored practical and collection management recommendations (Chapter 2), and I consider the latter first. Implicit in my finding here, is that the "thriftiness" enabling some species to succeed in their unpredictably varied wild environments, renders the same species prone to weight gain under well-provisioned captive conditions. This result may highlight a broad type of species at heightened risk of unwanted weight gain in captivity, including those outside this dataset: useful information when considering collection management. Thus, one might predict that other taxa with similarly unpredictable wild environments may also be prone to weight gain in captivity.

Next I consider practical recommendations for zoos, based on the potential risk factor I have identified here. Central to weight gain and obesity is positive energy imbalance, i.e. calorific intake greater than expenditure (Trayhurn, 1984; Selassie and Sinha, 2011). Besides genetic factors, such as those leading to the species' attributes and observed differences in the current study, energy balance is also affected by environmental factors e.g. diet and physical activity levels (Selassie and Sinha, 2011). Unlike genetics, the environment is more easily altered, so it is these I focus my recommendations on, most of which agree with suggestions made elsewhere. My results complement these previous works by uniquely identifying which particular species – the "thriftier" ones – might benefit most from these because of their natural lifestyle. Thus, I recommend that care is taken when designing captive diets to ensure that individuals are not overfed on calorie-rich diets (without restricting food *per se*; see next paragraph), especially for those of concern in Figure 5.3, and that feeding commercial fruit should be avoided (Goodchild and Schwitzer, 2008; Junge et al., 2009). When conditions dictate, many lemurs in the wild readily switch from a primarily fruit-based diet to other plant parts, e.g. leaves and flowers (Wright, 1999). Shifting captive diets away from fruit for most, if not all, species is therefore feasible and compatible with maintaining health (see also Junge et al., 2009). Increased exercise opportunities could also reduce weight in affected animals, especially those "thrifty" species (also see Taylor et al., 2012). Providing natural-type, flexible climbing materials (see also Section 5.4.1); encouraging

movement by placing food and other preferred resources such as enrichment in different areas and at various heights around the enclosure; and necessitating climbing and distances to be covered into enclosures at the initial design stage are all plausible, easily facilitated suggestions.

As unpredictability is key to the potential biological risk factor identified here, I would also recommend that zoos take steps to reduce cues that might signal captive food unpredictability. As already mentioned (Section 5.4), food provided in a small number of discrete meals rather than being constantly available might signal unpredictability (see also Sections 6.4 and 7.3), triggering behaviours and physiological processes that enable these species to survive in their unpredictable native environment (e.g. increased resting, reduced basal metabolic rate: Wright, 1999), resulting in weight gain when animals are fed energy-rich captive food. With this in mind, zoos might therefore consider either feeding animals more frequently, and/or providing *ad libitum* access to low-calorie food stuffs (cf. Nettle et al., 2017), e.g. by including mature live trees within enclosures to provide browse, as a complementary or alternative method to feeding rations in discrete meals. Doing so may help reduce potential binge-eating and dominance effects at feeding times; help reduce potential signalling of food unpredictability; and climbing trees to forage would also represent an exercise opportunity.

Finally, the across-species approach used here also helps direct species-specific work (e.g. Section 3.4.1). Figure 5.3 clearly highlights species whose typical captive body conditions are concerning, because they deviate the most from their wild norms, i.e. common brown lemurs, blue-eyed black lemurs, crowned lemurs, black lemurs, and ring-tailed lemurs. As mentioned in Section 5.4, I would therefore recommend that research effort is targeted towards these priority species.

5.4.2 Future research

In terms of future work based on the potential biological risk factor identified here and associated recommendations (see Section 5.4.1), research should be aimed at improving understanding the relationship between the risk factor possibly identified here, weight gain and the captive feeding environment. Is it that animals from "thrifty" species are simply easier to overfeed? Or is it the case that somehow food unpredictability is being signalled? Effects of feeding discrete meals *versus ad libitum* feeding, and the number of meals on animals' behaviour and body mass; assessing if animals display behavioural and/or physiological reactions in line with food resource unpredictability having been signalled to them, e.g. increased resting (cf. Wright, 1999); and investigating if some animals really do binge-eat are all relevant topics, that would be informative to zoos and their management of lemurs.

Relative body mass's thresholds used here as a proxy for body condition now require validation, with two main questions to address. As mentioned above if there is considerable within-species variation in body size *not* linked with fatness, i.e. length, then relative body mass may not be a true representation of body condition. Logically, taller animals are likely heavier than shorter ones, which could result in large relative body masses reflecting their body size but *not* condition, i.e. fatness. Quantifying within-species length variation is thus crucial in establishing whether relative body mass works as a 'one size fits all' method of inferring body condition as is currently assumed. If not, a body mass index method might be more appropriate, although this too would require validation for lemurs. Secondly, the accuracy of Taylor et al. (2012)'s threshold for obesity (relative body mass ≥1.5; 50% greater than the wild mean) requires assessment, partly because it is conservative compared to thresholds at which obesity-related health problems are observed in other taxa (20-25% over the ideal, e.g. Kealy et al., 2002; Selassie and Sinha, 2011; Laflamme, 2012). If reliable, one would predict animals classed as obese would have reduced life expectancy, and higher incidences of comorbid health problems like cardiac disease, diabetes, and supressed reproduction (e.g. Kopelman, 2000; Hatt and Clauss, 2006; Bauer et al., 2011; Laflamme, 2012; Vaughan and Mattison, 2016; RSPCA, 2019). As outlined in Chapter 2, using pre-

existing zoo records of animals' weights, veterinary records, and dates and cause of death could facilitate this (e.g. as held in Species360's Zoological Information Management Software database: Species360, 2018). Morphometric measurements known to reliably indicate obesity in other species could prove useful, such as skinfold thickness measurements e.g. at the abdomen (e.g. Dittus and Gunathilake, 2015), including opportunistically quantifying adipose tissue at post-mortem (e.g. Pereira and Pond, 1995).

Validating relative body mass's obesity threshold would also help address whether the 'obesity' described in some lemurs is truly obesity, in a pathological sense, because current evidence is rather mixed. That ring-tailed lemurs, typically overweight in this and Taylor et al. (2012) studies, are apparently prone to diabetes (Kuhar et al., 2013) is in line with what one would predict in an obesity-prone species. Additionally, obesity is often cited as explaining poor reproduction in captive lemurs (e.g. Schaaf and Stuart, 1983; Pereira and Pond, 1995). To the best of my knowledge, however, relationships between 'obesity' and reproduction or, indeed, any other related health outcome have never been formally investigated. Furthermore, one study on ruffed lemurs in European zoos in fact found a positive correlation between female body weight and reproductive output (Schwitzer and Kaumanns, 2009), with heavier females producing larger, more frequent litters annually, rather than the more typical biannual wild litter (Goodchild and Schwitzer, 2008; Schwitzer and Kaumanns, 2009). Increased provisioning of semi-wild ring-tailed lemurs also resulted in >40% more twin births (Pereira, 1993). Reproductive output is closely linked to maternal nutrition and condition (Hume, 1995). Therefore, it is not implausible that the body masses observed in Schwitzer and Kaumanns (2009)'s study could be within the 'healthy' range for those species, with increased reproductive output representing a reaction to times of plenty. Alternatively, as already described here it might be that the heavier females in Schwitzer and Kaumanns (2009)'s study were simply longer-bodied, and their weights could have been healthy for their frames. Finally, it might be that such "thrifty" species are able to carry relatively greater fat-stores safely, without it being determinantal to health – indeed, to do so would seem to be adaptive, for wild animals at least. If this were the case, then using obesity thresholds based other taxa (20-25% over the ideal in dogs, cats and humans: Kealy et al., 2002; Selassie and Sinha, 2011; Laflamme, 2012) would not be appropriate, and

even Taylor et al. (2012)'s ≥50% of species-typical wild mean might prove to be inappropriate.

As already discussed, living conditions affect an individual's body condition, e.g. diet and exercise opportunities (Selassie and Sinha, 2011). In the current study, I did not control for husbandry effects in my models, as none of my species-typical husbandry variables correlated with my wild predictors (see Section 5.3.2). However, even if I had these were at the *species*- rather than *individual*-level. Low R^2 values are common in comparative studies (Freckleton, 2009), and this was true of my model with the trend (inter-year annual rainfall CV model: R^2=0.288; see Table 5.6). This leftover unexplained variance might, potentially, be explained by individual-level effects that a comparative analysis is not sensitive to. Additionally, in this chapter I was unable to examine sex differences regarding relative body mass, as for many species I did not have ≥ 5 animals within each sex (the minimum requirement for a species' inclusion in analyses: Section 5.2.1.2). In other primates, there are sex differences in obesity-risk, ease of weight loss, pattern of fat storage, and weight-related health problems (Power and Schulkin, 2008; Ely et al., 2013; Obanda et al., 2014). Therefore, taking an epidemiological approach to examine individual-level living conditions and demography could be valuable (cf. Section 2.1), and this is what I do in Chapter 6.

Finally, obesity is not a problem restricted to lemurs. Many other primate species, including humans, are prone; far more so than other taxa, including carnivores (Pereira and Pond, 1995; Schwitzer and Kaumanns, 2001). Primates are suggested to have evolved adaptations to protect against starvation with defences for stored body fat, to ensure they have supplies to feed a relatively large and expensive brain (Shively et al., 2009). Following from this, I would hypothesise that across Primates, these adaptations ensuring adequate resource availability for large, energetically expensive brains might explain susceptibility to captive weight gain. If this is true, then species with the largest brains should be most obesity-prone in captivity.

5.5 Conclusions

In this chapter, I found partial support for one hypothesis: that captive weight gain relates to physiological adaptations to unpredictable food resource availability within the native range. Thus, species that experience large inter-year variation in annual rainfall, and greater food resource unpredictability, tend to have larger species-typical relative body masses. This aspect of species-typical biology, therefore, can be considered a potential biological risk factor for susceptibility to captive weight gain, but this finding requires replication. My results demonstrated some good, though not total, agreement with similar previous multi-species studies. Some species showed striking consistencies in typical body condition: concerning for the species found to be persistently large across studies, who should now be prioritised for research effort. Validation of relative body mass as a body condition proxy; establishing whether the 'obesity' observed in some animals is obesity in the pathological sense; and whether individual-level environmental effects might better explain animals' susceptibility to captive weight gain are all avenues for future research.

Chapter 6: Risk factors for overweight captive lemurs: an epidemiological approach

Abstract

Animals with excessive body masses, i.e. those overweight or obese, can suffer related health problems. In some lemur species, captive individuals are prone to being overweight or obese (defined as a 'relative body mass' 1.25 and 1.5 times species-typical wild means respectively), representing a health concern. In Chapter 5, I uncovered a trend for a potential biological risk factor for increased relative body masses in captive lemurs. Thus, species that experience unpredictable food resources in the wild, as inferred by inter-year variation in annual rainfall within native ranges, tended to have large relative body masses. Aside from species-typical biology, weight is also affected by living conditions and demographics. In this chapter, I used epidemiological approaches to examine potential living-condition and demographic risk factors for increased relative body mass across four species: ring-tailed lemurs, *Lemur catta*, mongoose lemurs, *Eulemur mongoz*, and black-and-white ruffed and red ruffed lemurs, *Varecia variegata* and *rubra*. I tested hypotheses relating increased relative body mass to reduced exercise/activity opportunities, contraceptive use/neutering, and feeding a high proportion of fruit. I used an online survey to collect body masses (for relative body mass calculations), corresponding living conditions and demographic information (predictor variables) for 544 zoo-housed adult lemurs from the four species mentioned above. Relative body mass was calculated as the ratio of a captive animal's body mass to its species-typical wild mean. I explored relationships between relative body mass and my predictors using mixed effects models. Species differed in relative body mass values, and older lemurs were larger. I also found an interaction between species and sex. Thus, female mongoose lemurs were heavier than males and typically overweight, and male ring-tailed lemurs were heavier than females, with both

sexes on average overweight. In partial support of my exercise/activity hypothesis, males housed in enclosures with only fixed climbing structures have larger relative body masses (typically obese) than those housed with a mixture of flexible and fixed structures. Finally, female relative body mass values varied seasonally. Based on my results, I detail targeted recommendations to mitigate weight problems in affected animals, and describe directions for future research to better understand why certain individuals and groups are at risk.

6.1 Introduction

Animals with excessive body masses, i.e. those overweight or obese, can suffer related health problems (Laflamme, 2006; WHO, 2019). Here, I define being overweight or obese as a relative body mass ≥1.25 and ≥1.5 times, respectively, the species-typical norm (after for e.g. Taylor et al., 2012; and reviewed in detail in Chapter 5). Obesity in particular is co-morbid with other serious health problems in humans and non-human animals, e.g. metabolic syndrome, diabetes, heart disease, impaired reproduction, orthopaedic disorders, cancers and reduced lifespan (Kopelman, 2000; Hatt and Clauss, 2006; Bauer et al., 2011; Laflamme, 2012; Vaughan and Mattison, 2016; RSPCA, 2019). In 2016, the prevalence of overweight and obese adult humans worldwide was 39% and 13%, respectively, and this is increasing (Ogden et al., 2006): the latter's prevalence has almost tripled since 1975 (WHO, 2019). A similar trend is reported in human-managed animals too, such as pet cats, *Felis catus*, and dogs, *Canis lupus familiaris* (German, 2006), horses, *Equus caballus* (Johnson et al., 2009), and other species living in close proximity to humans, e.g. laboratory primates and rodents and feral rats, *Rattus norvegicus* (Klimentidis et al., 2011).

In Chapter 5 I investigated relationships between potential biological risk factors for increased relative body masses (i.e. the captive body mass as a ratio of the species-typical mean, after: Taylor et al., 2012) across 13 captive lemur species. I found that unpredictable food resources in the wild, as inferred by inter-year variation in annual rainfall within the native range, tended to positively correlate with relative body masses. Implicit in this result, is that adaptations for "thriftiness" (sensu Neel, 1962) that likely allow some lemur species to succeed in the wild, place the same species at risk of weight gain in captivity (Chapter 5). However, there was no strong support for any one hypothesis and, as is common in comparative analyses (Freckleton, 2009), the R^2 for the model with the trend was relatively low (=0.274; see Table 5.6). An individual's energy balance, and thus risk of weight gain, is also affected by their living conditions and demographic (e.g. Selassie and Sinha, 2011). Therefore, some aspect of living conditions might contribute more to weight variation in captive lemurs than does species-typical biology.

Epidemiology is the study of the distribution and risk factors of a health-related outcome across a population (Coggon et al., 2003). Animal health and welfare studies have used this approach to identify risk factors for, e.g. stereotypic behaviour in zoo elephants (Greco et al., 2016), *Loxodonta africana* and *Elephas maximus*; pre-weaning mortality in pigs, *Sus scrofa* (KilBride et al., 2014); and obesity in pet dogs and cats (McGreevy et al., 2005; Courcier et al., 2012). Identified risk factors enable targeted recommendations and strategies to be put into place to address the outcome of interest, and help improve understanding of why certain individuals are at risk (Coggon et al., 2003). As an illustration, poor diets, e.g. processed and sugar-sweetened foods, and a sedentary lifestyle are well-known risk factors for human obesity (Hruby and Hu, 2015), as is being neutered in cats and dogs (McGreevy et al., 2005; Courcier et al., 2012). In the human example, recommendations to help mitigate obesity risk might be to avoid those types of food and increase activity levels; and owners of neutered cats and dogs could be advised to take extra care to monitor weight and dietary intake in their neutered pets.

Of the species I collected data for in Chapter 5, four were relatively well-sampled regarding outcome data and corresponding living conditions. Thus, for these species their data represent a good opportunity to examine individual-level risk factors for increased relative body mass, using an epidemiological approach. In this chapter I aim to explore effects of husbandry-related measures (i.e. living conditions) and demographics (e.g. species and sex effects) on relative body masses across these four species.

Within my survey (see Appendix 6), I collected data on specific aspects of individuals' captive environment, because of their potential to affect/relate to body weight. These were: enclosure size and outdoor access; the nature of climbing structures; enrichment provision; diet; and contraceptive use/neuter status. If enclosure space is used to infer quality of usable space for exercise, then larger enclosures might represent greater exercise opportunities, and so energy expenditure (sensu Selassie and Sinha, 2011), than smaller ones. Types of enclosures likely differ in their thermoregulatory requirements which, again, affects energy expenditure and balance (sensu Campbell et al., 2008). Outdoor enclosures

likely have greater temperature ranges than indoor ones, and thus require their occupants to invest relatively more energetically to thermoregulation (sensu Campbell et al., 2008)**.** Enclosure furnishings, i.e. climbing structures and enrichment provision, could also affect animals' exercise opportunities and activity levels, and therefore energy expenditure (sensu Selassie and Sinha, 2011)**.** Unstable and flexible climbing structures (e.g. tree branches and ropes) likely require more physical effort, and energy expenditure, to climb than those stable and fixed in place (e.g. platforms and ladders); and if more enriched lemurs are more active because of these enrichments, then these too could affect body weight through increased energy expenditure (sensu Campbell et al., 2008). Unenriched American mink, *Neovison vison*, were found to eat more food rewards than enriched ones, consistent with the idea that unenriched mink were 'bored' (Meagher and Mason, 2012). Plausibly, a similar effect might be found in unenriched lemurs too, which could lead to weight gain. In addition to these physical aspects of the environment, my survey collected data on two further aspects of husbandry that might affect an animal's weight. Hormonal **c**ontraceptive use is associated with weight gain in primates (Portugal and Asa, 1995) including lemurs (Terranova and Coffman, 1997), and castration can induce obesity in other taxa (Trayhurn, 1984). Finally, commercial, domesticated fruit are more energy-rich than the fruits wild lemurs consume – hypothesised to explain the excessive body weights of some zoo lemurs (Goodchild and Schwitzer, 2008).

Therefore, in this chapter I test the following hypotheses:

i. Limited opportunity for exercise/activity leads to weight gain.
   → *Prediction*: animals whose captive environment provides the fewest exercise/activity opportunities should have the largest relative body mass values.
ii. Using contraceptives or neutering leads to weight gain.
   → *Prediction*: animals given contraceptives or who are neutered should have the largest relative body mass values.
iii. Feeding large proportions of fruit leads to weight gain.

→ *Prediction*: animals fed the highest proportion of fruit should have the largest relative body mass values.

Several demographic factors might also contribute to an individual's body weight. As demonstrated in Chapter 5 and elsewhere (Terranova and Coffman, 1997; Taylor et al., 2012), lemur species differ in their susceptibility to weight gain in captivity. In other primates, the sexes differ in risk of weight gain, their ease of weight loss, pattern of fat storage, and weight-related health problems (Power and Schulkin, 2008; Ely et al., 2013; Obanda et al., 2014). Older animals are at higher risk of weight gain in other primates (Bauer et al., 2011), although very old animals nearing the end of their lives might instead be lighter due to effects of chronic illness and other age-related complications (sensu Zehr et al., 2014). Finally, some wild lemurs' body masses fluctuate seasonally (e.g. Lewis and Kappeler, 2005; Simmen and Rasamimanana, 2018), as do those of captive animals (Zehr et al., 2014). Therefore, I also explored potential species, sex, age and seasonality effects on relative body mass.

6.2 Methods

As my unit of measurement in this chapter is 'individual' rather than 'species', I used the processed lemur survey dataset described in Chapter 5 (i.e. the individual-level responses to the survey, rather than the summarised species-typical values shown in Table 5.2). I focussed on the four best-sampled species (n): ring-tailed lemurs, *Lemur catta* (351), black-and-white ruffed lemurs, *Varecia variegata* (89), red ruffed lemurs, *V. rubra* (75), and mongoose lemurs, *Eulemur mongoz* (29). Early exploratory analyses did include other species featured in Chapter 5, but for all but these four there were too many missing cases in variables and levels for models to run successfully. Again, I focussed my analyses on non-pregnant, adult animals. I discarded entries from animals of unknown sex (one animal).

6.2.1 Outcome variable

As detailed in Chapter 5, my outcome variable was relative body mass. For each captive animal I calculated the ratio between its body mass and its species-typical wild mean, to yield its relative body mass. Relative body mass values were used to infer body condition using the following thresholds (after Taylor et al., 2012):

- → Underweight: relative body mass values of <0.75 represent the captive animal being less than 75% of its species-typical wild mean
- → Healthy: relative body mass values of 0.75-1.25 correspond with an animal being 75-125% of its species-typical wild mean
- → Overweight: relative body mass values of 1.25-1.5 correspond with an animal being 125-150% of its species-typical wild mean
- → Obese: relative body mass values of 1.5-2 correspond with an animal being 150-200% of its species-typical wild mean
- → Morbidly obese: relative body mass values of 2 or more correspond with an animal being twice the size (or more) of its species-typical wild mean

Using weight alone to infer body condition comes with the problem that an animal's frame is not controlled for (e.g. as it is in indices like body mass index; NHS, 2019). For instance, a healthy but very long animal is likely relatively heavier than a healthy but shorter one, and so the former's body condition may be over-estimated. However, data on each animal's body length were not available and, as taking such measurements on captive wild animals requires a degree of handling, are unlikely to become routinely recorded.

6.2.2 Predictor variables

Husbandry-related and demographic predictor variables were calculated from survey responses.

Husbandry-related predictors: Hypothesis i

a. Enclosure area

Continuous (m^2). Ranged from 5-57,884.54 m^2.

This variable was the total enclosure area (m^2) reported by respondents (i.e. summed across indoor and outdoor enclosures where relevant).

If my data support this hypothesis, then animals in smaller enclosures should have larger relative body masses. Data were available for 469 animals (302 ring-tailed lemurs; 78 black-and-white ruffed lemurs; 60 red ruffed lemurs; 29 mongoose lemurs).

b. Enclosure type

Ordinal with three ranks: indoor only, indoor and outdoor, outdoor only.

Enclosures reported as indoor only or outdoor only were scored as such. Animals with access to indoor and outdoor enclosures for all or part of the year, or any combination of these were scored as 'indoor and outdoor'. These levels were ranked according to increasing need for thermoregulation (and therefore energy expenditure, sensu: Campbell, 2008): indoor only< indoor and outdoor<outdoor only.

If my data support this hypothesis, then relative body masses of animals should be largest in those housed indoors only, smallest in those that live entirely outside, and mid-way for those with indoor and outdoor enclosures. Data were available for 544 animals (351 ring-tailed lemurs; 89 black-and-white ruffed lemurs; 75 red ruffed lemurs; 29 mongoose lemurs).

c. Climbing structures

Categorical with two levels: fixed only; flexible and fixed.

Respondents described the types of climbing structures in their animals' enclosures. 'Fixed' climbing structures were those rigid and fixed into place, e.g. platforms, bolted down logs;

'flexible' referred to those unstable and flexible, e.g. ropes, branches on a living tree. For animals with indoor and outdoor enclosures, I scored their climbing structures as 'flexible and fixed' if at least one of their enclosures had flexible climbing structures. Just one enclosure had flexible structures only, so I pooled this entry into the 'flexible and fixed' level.

If my data support this hypothesis, then lemurs in enclosures with fixed climbing structures only should have larger relative body masses. Data were available for 544 animals (351 ring-tailed lemurs; 89 black-and-white ruffed lemurs; 75 red ruffed lemurs; 29 mongoose lemurs).

d. Enrichment score

Counts. Ranged from 0-22.

Respondents provided information on how frequently five subtypes of enrichment were provided: foraging-related, manipulable, olfactory, audio/visual, and training (see Appendix 6 for details). I turned these into scores for each subtype's provision: daily (5), two/three times per week (4), weekly (3), monthly (2), less than monthly (1), never (0). I summed across all subtypes' scores to yield a total enrichment score up to a maximum of 25. One might predict that different types of enrichment differ in their potential for encouraging activity; however, a broad range of devices were included within some subtypes, and some were non-mutually exclusive (e.g. puzzle feeders were considered foraging enrichments, but they also share characteristics of manipulable enrichment devices). Given that that one of the main aims of enrichment use in zoos is to make animals' lives more 'active' (EAZA, 2013), summing across subtypes as I have seems appropriate.

If my data support this hypothesis, I expect animals with smaller enrichment scores to have larger relative body masses. Data were available for 544 animals (351 ring-tailed lemurs; 89 black-and-white ruffed lemurs; 75 red ruffed lemurs; 29 mongoose lemurs).

Husbandry-related predictors: Hypothesis ii

a. Contraceptive use/neutered

Categorical with two levels: yes, no.

If my data support this hypothesis, then animals given contraceptives or who are neutered should have larger relative body masses. Data were available for 491 animals (323 ring-tailed lemurs; 82 black-and-white ruffed lemurs; 64 red ruffed lemurs; 22 mongoose lemurs).

Husbandry-related predictors: Hypothesis iii

a. % fruit

Percentage. Ranged from 0-72.16%

From the amounts (in grams) described on diet sheets or entered directly into the survey, I calculated the percentage of each animal's diet that was fruit. Data were available for 529 animals (340 ring-tailed lemurs; 85 black-and-white ruffed lemurs; 75 red ruffed lemurs; 29 mongoose lemurs).

Demographic predictors

a. Species

Categorical with four levels: ring-tailed lemur, black-and-white ruffed lemur, red ruffed lemur, mongoose lemur.

Data were available for 544 animals (351 ring-tailed lemurs; 89 black-and-white ruffed lemurs; 75 red ruffed lemurs; 29 mongoose lemurs).

b. Sex

Categorical with two levels: female, male.

Data were available for 544 animals (351 ring-tailed lemurs; 89 black-and-white ruffed lemurs; 75 red ruffed lemurs; 29 mongoose lemurs).

c. Age at weighing

Continuous (days). Ranged from 929-12,097 days.

For animals with Zoological Information Management System (ZIMS) Specimen reports, I used these to calculate age at weighing. To boost sample sizes, by checking through previous correspondence with zoos I estimated some dates and corresponding seasons of weighing I had recorded as 'unknown' in Chapter 5. For these, I assigned the date of weighing as the 1st of whichever month the zoo had sent me weight records, and assigned the corresponding hemisphere-specific season of weighing using this date. For two animals with a date of birth but not a precise date of weighing, I also used these estimated dates to calculate estimated age at weighing. This resulted in these two being considered sub-adult, rather than adult as they were in Chapter 5, thus excluding them from analyses. Clearly, there is a certain degree of error associated with such estimations. However, ring-tailed lemurs are deemed adult from 978 days of age, and as these two were very close to adulthood (929 and 936 days), their inclusion in Chapter 5 is likely to have minimal impact. Maximum recorded captive lifespans of the four species are similar and thus ages are directly comparable (i.e. mongoose lemur=36.2 years; ring-tailed lemur=37.3 years; red ruffed lemur=37.6 years; black-and-white ruffed lemur=39.4 years: Tacutu et al., 2017).

Data were available for 365 animals (244 ring-tailed lemurs; 56 black-and-white ruffed lemurs; 43 red ruffed lemurs; 22 mongoose lemurs).

d. Season of weighing

Categorical with four levels: spring, summer, autumn, winter.

For each entry I used dates of weighing and geographic location of the zoo to calculate hemisphere-specific seasons of weighing.

Data were available for 544 animals (351 ring-tailed lemurs; 89 black-and-white ruffed lemurs; 75 red ruffed lemurs; 29 mongoose lemurs).

6.2.3 Statistical procedure

All analyses were performed in R using mixed effects models in the packages 'lmer4' (Bates et al., 2015), and 'ordinal' (Christensen, 2019). To account for variance explained by non-independence between animals sharing enclosures, and enclosures within the same zoo, 'enclosure' was nested in 'zoo' as a random effect. My outcome variable, relative body mass, was natural log-transformed to better meet the requirements of linear modelling, as were two predictor variables because of their skew and hence leverage of high values: age and enclosure area. During hypothesis-testing, outliers with studentised residuals >+/-3 (e.g. after Jones and Purvis, 1997) were removed (four animals) as their inclusion meant that models' residuals did not pass a Shapiro-Wilks normality test.

Being non-experimental data I assessed the explanatory power of predictor variables (cf. Table 2 in Aho et al., 2014) by assessing model fit with and without a focal predictor using Akaike information criterion (AIC) scores (Akaike, 1973). Models with lower AIC scores by ≥2 were judged as improvements (Burnham and Anderson, 2004), and if two candidate models were within 2 AIC scores of one another I chose the simplest (Crawley, 2013). If the full model with the focal predictor was a better fit to the data, I assessed the nature of the relationship using the model's coefficients. When this included categorical predictor terms with more than two levels, I spilt the dataset by that factor and re-ran the analysis to fully assess the relationship between the focal predictor and outcome.

6.2.3.1 Relationships between predictors

Prior to hypothesis-testing, I checked for relationships between my predictors using all data available for each variable. For each model, using AIC I first assessed whether varying intercepts only or intercepts and slopes provided the better fit, with the random effects structure mentioned above. Linear mixed models were used for continuous outcome variables, i.e. age and enclosure size. Generalised linear mixed models (binomial family and logit link function) were used for binomial outcome variables (i.e. contraceptive use/neutered and sex), and for when % fruit (gamma family and inverse link function) and enrichment score (Poisson family and log link function) were analysed as outcome variables. When enclosure type was analysed as an outcome, I used cumulative link mixed models (probit link function) which facilitate analysis of ordinally ranked outcomes (Christensen, 2019). Relationships between variables were confirmed if the full model with the predictor term was a better fit (lower AIC scores by ≥2) to the data than null without it (Crawley, 2013). For predictors found to be related, I ran additional models at the univariable stage of hypothesis testing (below) to assess the potential effect(s) of correlated predictor(s).

6.2.3.2 Hypothesis-testing

To enable model comparisons, I reduced my dataset to animals with complete data across all variables. I followed a similar model-building approach to KilBride et al. (2014), though using AIC rather than P values to assess relationships and, unlike them, I did assess interactions. I first checked for univariable associations between my predictors and outcome. I used linear mixed models with the same previously mentioned random effects structure, and assessed first whether varying intercepts only or slopes and intercepts were necessary (in practice, varying intercepts and slopes never gave a better fit, as determined by AIC, than varying intercepts only). Univariable relationships between predictors and relative body mass were confirmed if the full model with the focal predictor term was a better fit (lower AIC scores by ≥2) to the data than null without it (Burnham and Anderson, 2004; Crawley, 2013). I ran additional models including previously identified correlated predictors as extra terms, to check that their relationship did not explain the association between the focal predictor and relative body mass. Predictors found to have a univariable

relationship with relative body mass were taken forward to the multivariable model-building stage.

Multivariable model building began with a model including all predictors with a univariable association with relative body mass. I used a forwards multiple regression technique and made comparisons to the simplest version of this model (i.e. without any interactions) to check for improvements in model fit by progressively including interactions, stopping when additions did not yield further improvements. This became my minimal adequate (baseline) model. Using this baseline model, I then reassessed potential effects of predictor variables that previously did not have a univariable association with relative body mass (after Cox and Wermuth, 1996; KilBride et al., 2014). I sequentially added these predictors back into the baseline model, again checking for interactions, to see if they now improved model fit further. I continued until none of the remaining predictors resulted in improvements, yielding my final minimal adequate model.

6.3 Results

6.3.1 Descriptive results

Five hundred and forty-four animals, 233 females and 311 males, had data for one or more variables. Relative body mass values ranged from 0.68-2.06. Using the thresholds for body condition as described in Chapter 5 0.37% (2/544) of individuals were underweight (relative body mass<0.75); 57.54% (313/544) were healthy (0.75-1.25); 27.76% (151/544) were overweight (1.25-1.5); 14% (76/544) were obese (1.5-2); and 0.37% (2/544) morbidly obese (≥2) (body condition thresholds based on: Taylor et al., 2012).

6.3.2 Between-predictor checks

Results of between-predictor checks are shown in Table 6.1. The following predictor variables were found to be related:

When sex was the outcome variable, the models including contraceptive use/neutered and season as predictors were better fits to the data than the null. Animals given contraception were less likely to be male (Z=-2.91, P<0.01); and animals weighed in spring were more likely to be male (autumn *versus*: spring: Z=2.98, P<0.01; summer: Z=-1.06, P=0.29; winter: Z=0.80, P=0.42).

For the age models, the model with species as a predictor was a better fit to the data than the null. Ring-tailed lemurs were younger than mongoose lemurs ($t=_{241}$-2.34, P=0.02), as were, to a lesser extent, black-and-white ruffed lemurs (t_{241}=-1.73, P=0.08; red ruffed v mongoose lemurs: t_{241}=-0.65, P=0.52).

For the contraceptive use/neutered models, the models with enrichment score and percentage fruit as predictors were better fits to the data than the null. Animals in more enriched enclosures were more likely to be given contraception/neutered (Z=3.39, P=0.001); and animals fed less fruit were more likely to be given contraception/neutered (Z=-2.71, P=0.01).

For the enclosure area models, models including species, season, enclosure type, climbing structures, and enrichment score as predictors were all better fits than the null. Compared with mongoose lemurs, red ruffed lemurs were housed in larger enclosures (mongoose lemur *versus*: red ruffed lemurs: t_{315}=-1.86, P=0.063; ring-tailed lemurs: t_{315}=0.64, P=0.52; black-and-white ruffed lemurs: t_{315}=0.55, P=0.58). Animals weighed in the spring (t_{315}=-3.67, P<0.001), summer (t_{315}=-3.05, P<0.01), and winter (t_{315}=-7.00, P<0.001) had smaller enclosures than those weighed in the autumn. Indoor only enclosures were smaller than indoor and outdoor enclosures (indoor *versus* indoor and outdoor: t_{67}=-2.19, P=0.03; outdoor *versus* indoor and outdoor: t_{67}=-1.61, P=0.11). Enclosures featuring fixed climbing structures only were smaller (t_{68}=-2.21, P=0.03), and higher enrichment scores were also associated with smaller enclosures (t_{317}=-1037.32, P<0.0001).

For the enclosure type models, the model including species as a predictor was a better fit than the null. Compared with mongoose lemurs, both black-and-white ruffed and red ruffed lemurs were more often housed outdoors ($Z=3.88$, $P=0.0001$; $Z=4.78$, $P<0.0001$).

For the enrichment scores models, the model with enclosure type as a predictor was a better fit to the data than the null. Outdoor enclosures have higher enrichment scores compared with indoor and outdoor enclosures (outdoor *versus* indoor and outdoor: $Z=2.43$, $P=0.01$; indoor *versus* indoor and outdoor: $Z<0.01$, $P=0.99$).

Thus, predictors identified here as being related had their possible effects on focal predictors assessed during the univariable stage, by including these correlated terms in the relevant models.

Table 6.1 Results of between-predictor checks. Note that species and season, being categorical with >2 levels and nominal, were not analysable as outcome variables. In all cases, I first checked if varying intercepts only or intercepts and slopes were the best fit (the latter case being indicated with asterisks). Model comparisons were then made between the full model including the focal predictor and the null, using AIC (see Section 6.2.3.1). The AIC of the null model is reported first. Full models found to be a better fit to the data than the null are shown in bold. For these, I assessed the nature of the relationship between the predictor and the outcome using the model's coefficients and describe them in the text

Outcome: **Predictor:**	**Sex**	**Age**	**Contraceptive use/neutered**	**Enclosure area**	**Enclosure type**	**Climbing structures**	**Enrichment score**	**% fruit**
Species *Ref: Mongoose lemur*	AIC: 708.84 v 711.28, P=0.313	**AIC: 640.79 v 637.73, P=0.03**	AIC: 423.59 v 425.24, P=0.23	**AIC: -405.81 v -434.91, P<0.001**	**AIC: 94.61 v 86.60, P<0.01**	AIC: 40.63 v 45.88, P=0.86	AIC: 2775.40 v 2780.60, P=0.83	AIC: 3376.50 v 3377.90, P=0.21
Sex *Ref: Female*		AIC: 640.79 v 641.64, P=0.28	AIC: 300.71 v 302.57, P=0.72*	AIC: -413.46 v -412.53, P=0.30*	AIC: 94.61 v 96.18, P=0.51	AIC: 40.63 v 46.59, P=1	AIC: 2775.40 v 2777.30, P=0.73	AIC: 3376.50 v 3377.90, P=0.47
Age *(days)*	AIC: 484.64 v 485.31, P=0.25		AIC: 296.92 v 298.27, P=0.42	AIC: -190.50 v -191.78, P=0.07	AIC: 48.33 v 50.22, P=0.73	AIC: 22.46 v 24.46, P=0.98	AIC: 1870.70 v 1872.70, P=0.86	AIC: 2468.80 v 2467.60, P=0.39

Outcome: **Predictor:**	**Sex**	**Age**	**Contraceptive use/neutered**	**Enclosure area**	**Enclosure type**	**Climbing structures**	**Enrichment score**	**% fruit**
Season *Ref: Autumn*	**AIC: 708.84 v 699.01, P<0.01**	AIC: 640.79 v 640.31, P=0.09	AIC: 423.59 v 426.35, P=0.36	**AIC: -405.81 v -445.78, P<0.001**	AIC: 94.61 v 99.45, P=0.97	AIC: 40.63 v 46.58, P=1	AIC: 2775.40 v 2777.70, P=0.29	AIC: 3376.50 v 3379.90, P=0.47
Contraceptive use/neutered *Ref: No*	**AIC: 557.99 v 551.91, P<0.01***	AIC: 531.78 v 532.93, P=0.36		AIC: -451.96 v -452.54, P=0.11	AIC: 94.55 v 96.55, P=0.96	AIC: 40.58 v 42.23, P=0.55	AIC: 2532.60 v 2534.40, P=0.65	AIC: 2800.20 v 2800.40, P=0.19
Enclosure area *(m^2)*	AIC: 620.58 v 622.55, P=0.87	AIC: 569.46 v 571.32, P=0.84	AIC: 358.18 v 359.13, P=0.31		AIC: 61.79 v 62.44, P=0.25*	AIC: 36.79 v 35.71, P=0.08	AIC: 2385.00 v 2386.80, P=0.63	AIC: 2759.60 v 2761.40, P=0.65
Enclosure type *Ref: Indoor and outdoor*	AIC: 708.84 v 710.82, P=0.37	AIC: 640.79 v 642.23, P=0.28	AIC: 423.59 v 424.83, P=0.25	**AIC: -405.81 v -408.53, P=0.03**		AIC: 40.63 v 44.60, P=0.98	**AIC: 2775.40 v 2773.3, P=0.05**	AIC: 3376.50 v 3377.80, P=0.26

Outcome: **Predictor:**	**Sex**	**Age**	**Contraceptive use/neutered**	**Enclosure area**	**Enclosure type**	**Climbing structures**	**Enrichment score**	**% fruit**
Climbing structures *Ref: Flexible and fixed*	AIC: 708.84 v 710.61, P=0.63	AIC: 640.79 v 642.79, P=0.98	AIC: 423.59 v 425.58, P=0.95	**AIC: -405.81 v -408.61, P=0.03**	AIC: 94.61 v 96.60, P=0.97		AIC: 2775.40 v 2777.40, P=0.88	AIC: 3376.50 v 3378.50, P=0.99
Enrichment score *(0-25)*	AIC: 704.60 v 706.06, P=0.46*	AIC: 640.79 v 642.28, P=0.47	**AIC: 423.59 v 405.16, P<0.001***	**AIC: -405.81 v -2832.36, P<0.001**	AIC: 95.22 v 96.96, P=0.61*	AIC: 40.63 v 42.63, P=0.93		AIC: 3376.50 v 3376.10, P=0.13
% fruit *(0-100%)*	AIC: 690.20 v 690.38, P=0.18	AIC: 620.37 v 620.90, P=0.23	**AIC: 414.34 v 407.11, P<0.01**	AIC: -372.03 v -370.67, P=0.42	AIC: 96.30 v 98.07, P=0.64*	AIC: 40.62 v 42.35, P=0.60	AIC: 2697.80 v 2696.90, P=0.09	

6.3.3 Univariable results

The reduced dataset contained complete data for 256 animals. Predictors found to have a univariable association with relative body mass, along with model coefficients, are shown in Table 6.2. In sum, including species, sex, and age as predictors were found to individually result in better fits to the data than the null model. None of the other predictors had an univariable association with relative body mass. In all cases, previously identified correlated predictors were not found to explain the focal predictor's relationship with relative body mass.

Table 6.2 Details of predictor variables found to have a univariable relationship with relative body mass. Random effects were 'enclosure' nested in 'zoo'. For each predictor, varying intercepts but common slopes were found to be the best fit to the data. AIC $^{-185.23}$= AIC value of the null model (i.e. without predictor terms). P^{AIC}= P value of the comparison between the null and the full model with focal predictor. Coef.=coefficient. SE=standard error. df=degrees of freedom.

Predictor details			*Comparisons to null*		*Model coefficients*				
Predictor variable	**Levels**	**N of animals**	**AIC $^{-185.23}$ v**	**P^{AIC}**	**Coef.**	**SE**	**df**	**t**	**P**
Species	Black-and-white ruffed lemur	36	-206.70	<0.001	-0.17	0.06	169	-2.80	0.01
	Red ruffed lemur	22			-0.05	0.06	169	-0.78	0.44
	Ring-tailed lemur	183			0.03	0.05	169	0.49	0.62
	Mongoose lemur (ref)	15			-	-	-	-	-
Sex	Male	146	-189.18	0.01	0.05	0.02	171	2.45	0.02
	Female (ref)	110			-	-	-	-	-
Age	Days	256	-187.89	0.03	0.04	0.02	171	2.16	0.03

6.3.4 Multivariable results

The baseline model with the three predictors found to have a univariable association with relative body mass, is shown in Table 6.3. In addition, the interaction between species and sex was a better fit to the data than a simpler model without it (AIC=-211.93 v -216.09, P=0.02) and is likewise shown in Table 6.3.

My final minimal adequate model featured the following (see Table 6.4). Species and age both had main effects. Black-and-white ruffed lemurs had smaller relative body mass values than ring-tailed lemurs (t_{146}=-5.11, P<0.001) and red-ruffed lemurs (t_4=-3.94, P=0.02) (see Figure 6.1). and relative body mass increased with age (t_{157}=2.09, P=0.04; Figure 6.2). Across species, males had smaller relative body masses than females (t_{157}=-2.06, P=0.04; see Table 6.4), but there was a sex*species interaction (Figure 6.3). Male mongoose lemurs have smaller relative body masses than females (t_6=-2.76, P=0.03), whereas male ring-tailed lemurs have larger values than females (t_{127}=3.15, P<0.01).

After sequentially adding in other predictors that did not have univariable associations with relative body mass, interactions between two further predictors and sex featured in the final minimal adequate model. Males housed in enclosures featuring only fixed climbing structures had larger relative body masses than those with flexible and fixed structures (t_{157}=3.04, P<0.01; Figure 6.4). Females weighed in the winter had larger relative body masses than those weighed in spring (t_{178}=3.30, P<0.01) and summer (t_{25}=3.70, P<0.01; Figure 6.5).

Table 6.3 Details of baseline model featuring three predictors, with one interaction, all previously identified as having a univariable relationship with relative body mass. The sex*species interaction was found to be a better fit to the data than a simpler model without it (AIC=-211.93 v -216.09, P=0.02). Random effects were 'enclosure' nested in 'zoo'. For each predictor varying intercepts but common slopes were found to be the best fit to the data. Coef.=coefficient. SE=standard error. df=degrees of freedom.

Predictor details			*Model coefficients*				
Predictor variable	**Levels**	**N of animals**	**Coef.**	**SE**	**df**	**t**	**P**
Species	Black-and-white ruffed lemur	36	-0.22	0.08	164	-2.91	<0.01
	Red ruffed lemur	22	-0.10	0.08	164	-1.20	0.23
	Ring-tailed lemur	183	-0.05	0.07	164	-0.68	0.50
	Mongoose lemur (ref)	15	-	-	-	-	-
Sex	Male	146	-0.10	0.07	164	-1.47	0.14
	Female (ref)	110	-	-	-	-	-
Age	Days	256	0.05	0.02	164	2.60	0.01

Predictor details			***Model coefficients***				
Predictor variable	**Levels**	**N of animals**	**Coef.**	**SE**	**df**	**t**	**P**
Sex*Species	Male: Black-and-white ruffed lemur	22	0.14	0.09	164	1.60	0.11
Sex ref: female	Male: Red ruffed lemur	13	0.12	0.09	164	1.32	0.19
	Male: Ring-tailed lemur	103	0.17	0.07	164	2.39	0.02
	Male: Mongoose lemur (ref)	8	-	-	-	-	-

Table 6.4 Final multivariable model of predictors that explain relative body mass. Random effects were 'enclosure' nested in 'zoo'. For each predictor, varying intercepts but common slopes were found to be the best fit to the data (see Section 6.2.3.2). AIC $^{-216.08}$= AIC value of the baseline model. P^{AIC}= P value of the comparison between the baseline without and with the focal predictor term (the first four predictors are the baseline model itself, hence they do not have AIC values). Coef.=coefficient. SE=standard error. df=degrees of freedom. 95% CI^{LL}=lower 95% confidence interval of the coefficient; 95% CI^{UL}=upper 95% confidence interval of the coefficient.

Predictor details			***Comparisons to baseline model***		***Model coefficients***						
Predictor variable	**Levels**	**N of animals**	**AIC $^{-216.08}$**	**P^{AIC}**	**Coef.**	**95% CI^{LL}**	**95% CI^{UL}**	**SE**	**df**	**t**	**P**
Species	Black-and-white ruffed lemur	36	-	-	-0.22	-0.37	-0.08	0.08	157	-2.94	<0.01
	Red ruffed lemur	22			-0.10	-0.25	0.06	0.08	157	-1.20	0.23
	Ring-tailed lemur	183			-0.06	-0.19	0.06	0.07	157	-0.92	0.36
	Mongoose lemur (ref)	15			-	-	-	-	-	-	-
Sex	Male	146	-	-	-0.17	-0.32	-0.01	0.08	157	-2.06	0.04
	Female (ref)	110			-	-	-	-	-	-	-

Predictor details			***Comparisons to baseline model***		***Model coefficients***						
Predictor variable	**Levels**	**N of animals**	**AIC $^{-216.08}$**	**P^{AIC}**	**Coef.**	**95% CI^{LL}**	**95% CI^{UL}**	**SE**	**df**	**t**	**P**
Age	Days	256	-	-	0.04	<0.01	0.07	0.02	157	2.09	0.04
Sex*Species	Male: Black-and-white ruffed lemur	22	-	-	0.16	<-0.01	0.32	0.08	157	1.86	0.07
Sex ref: female	Male: Red ruffed lemur	13	-	-	0.13	-0.04	0.30	0.09	157	1.43	0.15
	Male: Ring-tailed lemur	103			0.21	0.07	0.35	0.07	157	2.78	0.01
	Male: Mongoose lemur (ref)	8			-	-	-	-	-	-	-
Climbing structures	Fixed	19	-214.66	0.45	-0.93	-0.24	0.06	0.08	27	-1.15	0.26
	Flexible and fixed (ref)	239			-	-	-	-	-	-	-
Season	Spring	37	-220.20	0.16	-0.11	-0.24	0.01	0.06	157	-1.76	0.08
	Summer	108			-0.04	-0.12	0.05	0.04	157	-0.83	0.41
	Winter	37			0.13	0.02	0.25	0.06	157	2.18	0.03

Predictor details			***Comparisons to baseline model***		***Model coefficients***						
Predictor variable	**Levels**	**N of animals**	**AIC $^{-216.08}$**	**P^{AIC}**	**Coef.**	**95% CI^{LL}**	**95% CI^{UL}**	**SE**	**df**	**t**	**P**
	Autumn (ref)	74			-	-	-	-	-	-	-
Sex*Climbing structures	Male: Fixed	9	-221.01	0.01	0.24	0.09	0.39	0.08	157	3.04	<0.01
	Male: Flexible and fixed (ref)	137			-	-	-	-	-	-	-
Sex ref: female											
Sex*Season	Spring	26	-226.70	0.01	0.09	-0.05	0.22	0.07	157	1.22	0.23
Sex ref: female	Summer	56			0.07	-0.02	0.17	0.05	157	1.46	0.15
	Winter	18			-0.15	-0.29	-0.01	0.07	157	-2.06	0.04
	Autumn (ref)	46			-			-	-	-	-

Figure 6.1 Between-species differences in mean relative body mass (log-transformed). Points indicate a species' mean relative body mass value, and the whiskers depict the upper and lower 95% confidence intervals. Dotted horizontal line indicates the point at which relative body mass=1 (i.e. the captive animal is the same weight as its species-typical wild mean; 0 on the log-scale); the short dashed line indicates the overweight threshold (≥1.25, or 0.22 on the log-scale); and the long dashed line indicates the obese threshold (≥1.5, or 0.41 on the log-scale). Significant between-species differences are shown with asterisks. Ring-tailed lemurs (t_{146}=-5.11, P<0.001) and red-ruffed lemurs (t_4=-3.94, df=4, P=0.02) have larger relative body masses than black-and-white ruffed lemurs.

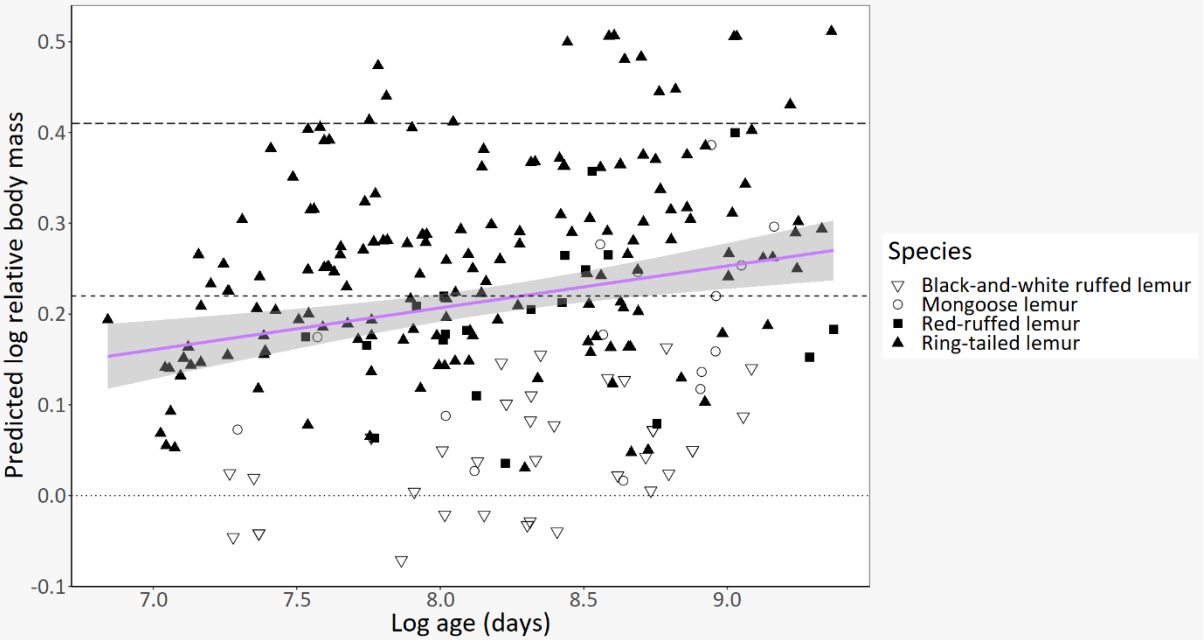

Figure 6.2 Relationship between relative body mass and age. Relative body mass increases with age (t_{157}=2.09, P=0.04) across four lemur species (both log-transformed). Dotted horizontal line indicates the point at which relative body mass=1 (i.e. the captive animal is the same weight as its species-typical wild mean; 0 on the log-scale); the short dashed line indicates the overweight threshold (≥1.25, or 0.22 on the log-scale); and the long dashed line indicates the obese threshold (≥1.5, or 0.41 on the log-scale). Note for ease of interpretation, the predicted rather than raw values of relative body mass are on the Y axis. The shaded area shows the 95% confidence region.

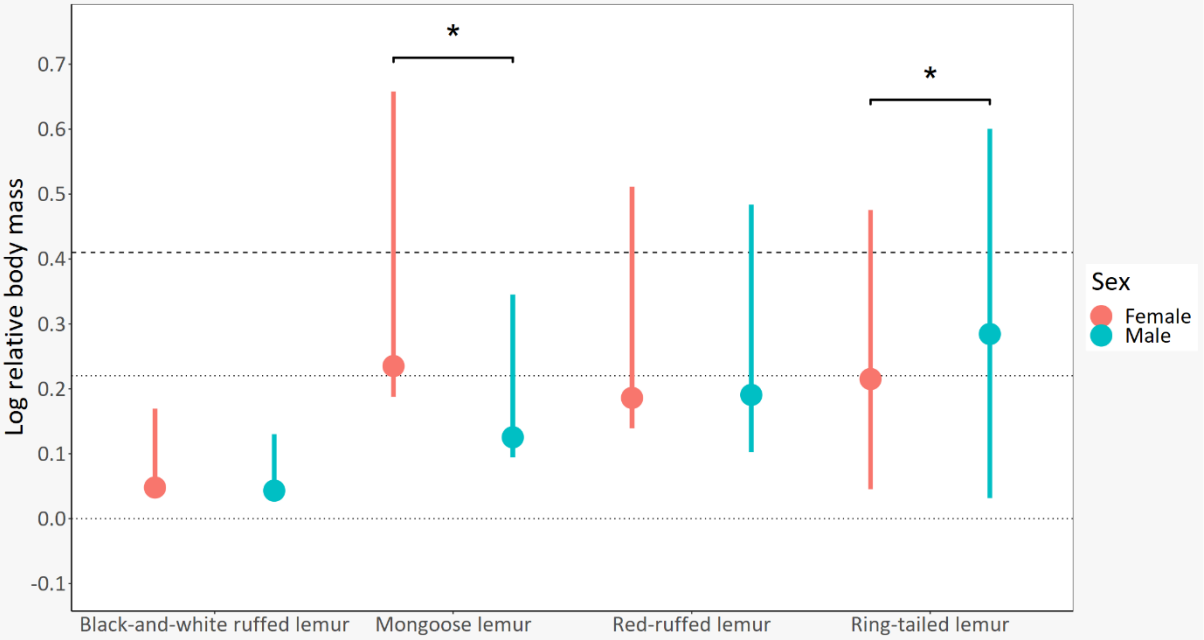

Figure 6.3 Relative body mass and the interaction between species and sex. Points indicate the mean relative body mass value of each sex within a given species, and the whiskers depict the upper and lower 95% confidence intervals. Dotted horizontal line indicates the point at which relative body mass=1 (i.e. the captive animal is the same weight as its species-typical wild mean; 0 on the log-scale); the short dashed line indicates the overweight threshold (≥1.25, or 0.22 on the log-scale); and the long dashed line indicates the obese threshold (≥1.5, or 0.41 on the log-scale). Within-species sex differences are indicated with asterisks. Male mongoose lemurs have smaller relative body masses than females (t_6=-2.76, P=0.03), whereas male ring-tailed lemurs have larger values than females (t_{127}=3.15, P<0.01).

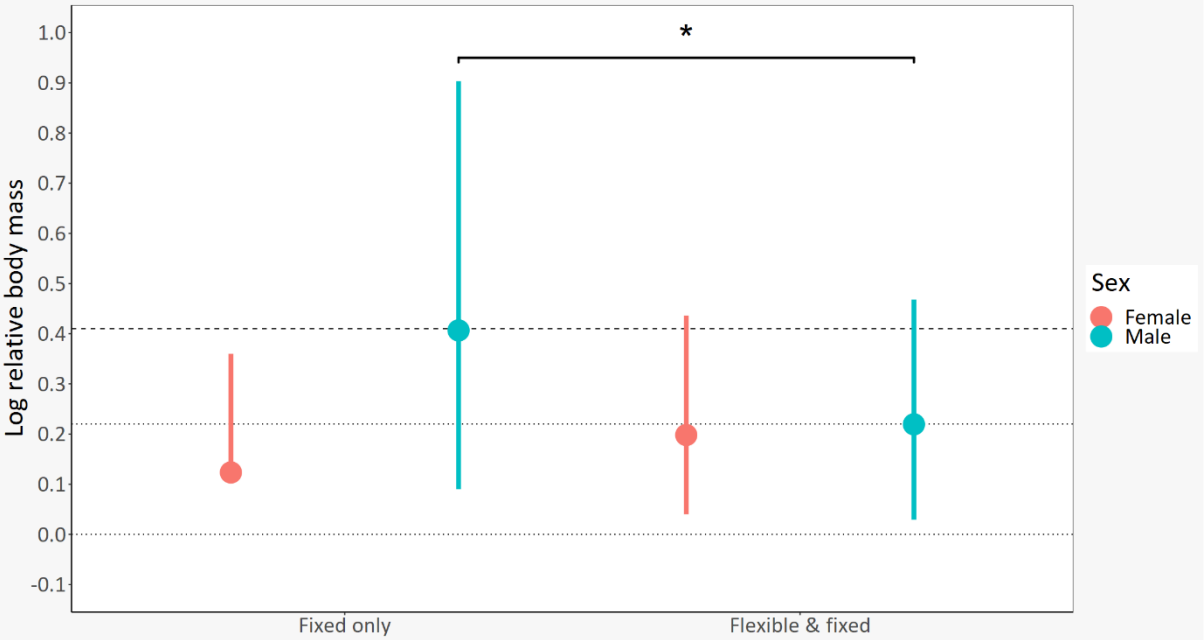

Figure 6.4 Relative body mass and the interaction between sex and provision of climbing structures. Points indicate the mean relative body mass value of each sex, split by climbing structure provision. Whiskers depict the upper and lower 95% confidence intervals. Dotted horizontal line indicates the point at which relative body mass=1 (i.e. the captive animal is the same weight as its species-typical wild mean; 0 on the log-scale); the short dashed line indicates the overweight threshold (≥1.25, or 0.22 on the log-scale); and the long dashed line indicates the obese threshold (≥1.5, or 0.41 on the log-scale). As indicated by the asterisk, males housed in enclosures featuring fixed climbing structures only (*versus* flexible and fixed structures) have larger relative body mass values (t_{157}=3.04, P<0.01).

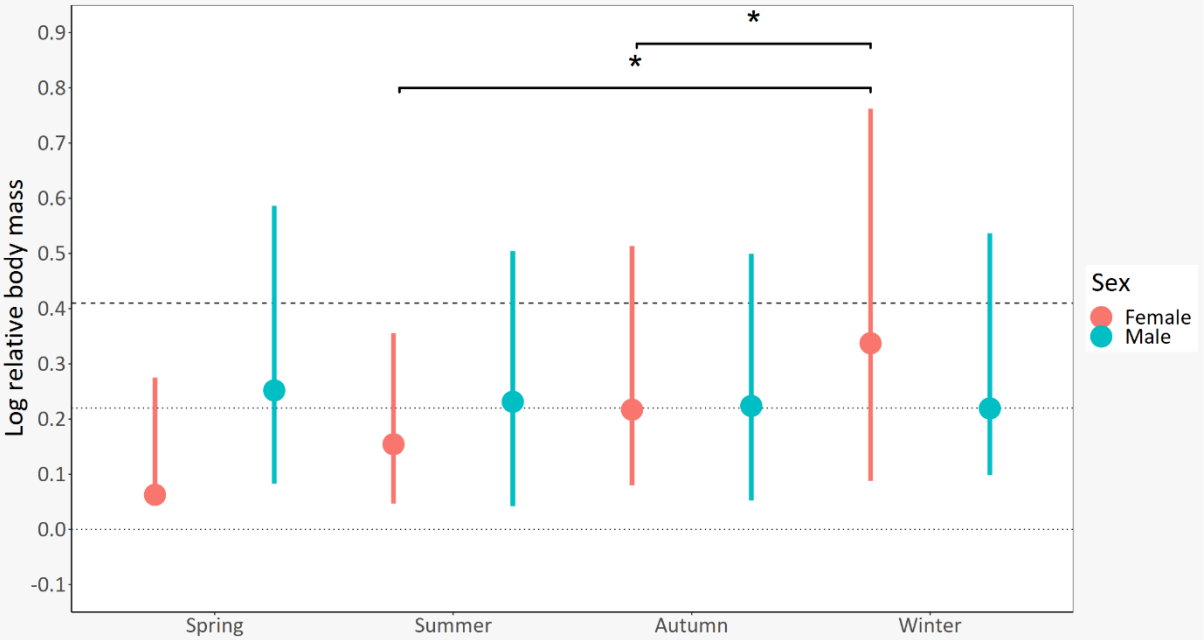

Figure 6.5 Relative body mass and the interaction between sex and season of weighing. Points indicate the mean relative body mass value of each sex split by the season weights were taken, whiskers depict the upper and lower 95% confidence intervals. Dotted horizontal line indicates the point at which relative body mass=1 (i.e. the captive animal is the same weight as its species-typical wild mean; 0 on the log-scale); the short dashed line indicates the overweight threshold (≥1.25, or 0.22 on the log-scale); and the long dashed line indicates the obese threshold (≥1.5, or 0.41 on the log-scale). Within-sex seasonal differences are indicated with asterisks. Females weighed in the winter had larger relative body masses than those weighed in spring (t_{178}=3.30, P<0.01) and summer (t_{25}=3.70, P<0.01).

6.4 Discussion

In this chapter I uncovered four demographic and one environmental risk factor for increased relative body masses across four lemur species. I confirmed, in line with what is reported in the literature (Terranova and Coffman, 1997; Taylor et al., 2012; and also Chapter 5), that there are between-species differences in average relative body masses and, inherently, propensity to conditions such as being overweight or obese (Figure 6.1). I also found an effect of sex: males and females of some species are not equally susceptible to having large relative body masses (Figure 6.3). Despite these overall species differences, however, the nature of climbing structure provision had an influence on relative body mass across males of all species (Figure 6.4), with no evidence for species differences in that effect. Thus, males have larger relative body masses when climbing structures are fixed,

compared with when at least some climbing structures within the enclosure are flexible. This result provides partial support for my hypothesis that limited exercise/activity opportunities leads to weight gain in captive lemurs, albeit only for males. I did not find support for my other two hypotheses relating to contraceptive use and feeding large proportions of fruit. Additionally, I also found that relative body masses increased with age, and that for females there are seasonal differences in relative body mass values (Figure 6.5). These attributes place certain individuals and groups at increased risk of having large relative body masses and, implicitly, increased risk of being overweight or obese. Therefore, extra care may be required to maintain healthy weight in affected animals. Next, I discuss each of these risk factors in turn, then describe the limitations of my study.

In agreement with Chapter 5 and works by others (Terranova and Coffman, 1997; Taylor et al., 2012) there was a main effect of species. Thus, ring-tailed and red ruffed lemurs had significantly larger relative body masses than do black-and-white ruffed lemurs (Figure 6.1). As found in Chapter 5, species-typical "thrifty" adaptations (sensu Neel, 1962) to environmental, and thus food resource, unpredictability might explain some of these species' differences. Of the four species in this study, ring-tailed lemurs have especially large relative body mass values (typically overweight i.e. >1.25, or >0.22 on the log-scale shown on Figure 6.1) and do experience relatively great wild resource unpredictability (see Figure 5.4). Further targeted research into why ring-tailed and red ruffed lemurs typically deviate so much from their wild average body mass is now required. As discussed in Chapter 5, fruitful avenues might include investigating the relationship between body length and relative body mass, and whether these species have greater propensity for fat-storage relative to other species (see Section 5.4.2).

For two species in my analyses there were sex differences in relative body mass (Figure 6.3). Female mongoose lemurs have significantly larger values (corresponding with overweight) than males (healthy), but in ring-tailed lemurs males were the heavier sex (but both sexes are considered overweight [Figure 6.3]). There are two possible explanations for this result. Firstly, this result could reflect sex-specific differences in body size. For outcome variable

calculations, I used mean species-typical wild body masses from Taylor and Schwitzer (2011), because sex-specific means were not available for every species in Chapter 5 (Section 5.2.1.2). Wild body masses of some species do show sex differences, and while these differences were not found to be statistically significant (Taylor et al., 2012) this could explain my result here. Another, more speculative explanation might relate to dominance hierarchy. Many prosimians, including the species in my study, are female dominant (Kappeler, 1999; Wright, 1999; White et al., 2007). In other taxa, under conditions of relatively low energy cost and high food availability, like those expected to be experienced in captivity, subordinate individuals maintain higher fat reserves than do dominants (e.g. Krams et al., 2010). Under such conditions, the nature of the trade-off between the risks of death from starvation and death from predation (Lima, 1986) differs according to an animal's place in the dominance hierarchy (Clark and Ekman, 1995; Ekman, 2004). Subordinates carry greater fat stores because they do not have feeding priority, and thus the risk of death due to starvation outweighs the increased risk of death by predation associated with carrying extra weight (Witter and Cuthill, 1993; Clark and Ekman, 1995). Logically, then, as most lemur species including the four in this study are characterised by female dominance (see Figure 1 in: Petty and Drea, 2015), we might indeed expect captive males to be the heavier sex. Across species, female ring-tailed lemurs are noted as being the most aggressive towards their males (Wright, 1999), so my result for ring-tailed lemurs is well in line with this. But, then, why is the *opposite* found here for mongoose lemurs, and the ruffed species also do not follow this pattern, yet ring-tailed lemurs do? A key assumption of the scenario described above, is that subordinate animals should only carry the most fat stores under certain conditions, i.e. those of relatively low energy cost and high food availability. Under other scenarios, dominants are those expected to carry greater fat stores (Ekman, 2004). Potentially then, there might be species differences in the perception of captive conditions explaining this result. For instance, if starvation risk is perceived as high; or predation risk is perceived as being less for dominant animals; or if food presentation and/or quality is signalled as being unpredictable (also see Sections 5.4, 5.4.1 and 7.3), one would expect dominant animals, i.e. females, to carry greater fat stores (sensu Ekman and Hake, 1990; Clark and Ekman, 1995; Ekman, 2004).

My analyses revealed an environmental risk factor for increased relative body mass in males: being housed with fixed climbing structures only (as opposed to with some flexible structures too) was associated with larger relative body masses (Figure 6.4). Opportunities for regular exercise/activity may affect weight via an animal's energy balance, and one can assume that climbing fixed structures requires less physical effort, and therefore less energy expenditure, than does climbing flexible structures (sensu Selassie and Sinha, 2011). Examining the body condition thresholds on Figure 6.4 shows that climbing structure provision appears to strongly affect male relative body mass. The mean relative body mass value for males housed with some flexible structures is on the overweight threshold; whereas the corresponding value for males housed with fixed only structures sits on the obese threshold. Considering the sex difference observed here, exercise-induced weight loss is reported to vary between the sexes in humans (Hagobian and Evero, 2013). Generally, when undertaking the same exercise males expend more energy than females, because they are usually larger-bodied and have larger total daily energy expenditure (Hagobian and Evero, 2013). A similar effect could explain why male lemurs, and not females, seem more affected by exercise opportunities. Alternatively, the effect I found here could be related to the female-dominant social structure of all the species within my dataset (Kappeler, 1999; Wright, 1999; White et al., 2007). Assuming that climbing structures are more preferred as a substrate than is the ground, fixed structures might be easier for dominant animals (i.e. females) to monopolise and exclude subordinate animals (i.e. males) from. Similar dominance effects might also explain the differences in substrate use by squirrel monkeys, *Saimiri sciureus sciureus*, in Marriott and Meyers (2005). Here, the two lowest ranking animals were the only two to spend their time mostly on the ground or in feeding areas, rather than on the preferred substrate (suspended logs) of their 10 higher ranking cage mates. Alternatively still, my result might be explained by other sex differences in climbing structure use and preference (e.g. female chimpanzees, *Pan troglodytes*, used elevated areas more than males, perhaps to avoid the males' displays: Traylor-Holzer and Fritz, 1985). Further research is therefore required to establish why climbing structure provision affects the relative body masses of the sexes differently, this best informing enclosure design to suit both sexes and support health. However, my result does indicate that, potentially, providing a mixture of flexible and fixed climbing opportunities to otherwise healthy lemurs,

regardless of sex, might be a feasible and easily implemented way to help address weight concerns.

Age also had a main effect: older animals had larger relative body mass values (Figure 6.2). This is in good agreement with other studies of weight-gain and age in non-human primates (Hansen, 2001) and human studies (inferred using body mass index: Thorpe and Ferraro, 2004). Examining Figure 6.2 suggests that the older half of my sample are more likely to be overweight, but that the regression line does not cross the obesity threshold. In other words, for these animals increasing age does not seem to pose a strong risk for obesity. However, it should be noted that most of the animals in my sample were relatively young. Indeed, only 14% (37/256) of them were ≥50% of their species-specific maximum recorded captive lifespan. Therefore, I cannot determine what effect increasing age beyond those sampled here may have on overweight or obesity-risk. Obesity in humans and non-human primates is linked with accelerated effects of aging (Vaughan and Mattison, 2016) and increased mortality (Thorpe and Ferraro, 2004). Furthermore, in humans obesity in *earlier* life is the bigger risk factor for increased mortality, while being slightly overweight in later life is actually protective, and associated with decreased mortality (Thorpe and Ferraro, 2004). Therefore, further research is now required to determine the health relevance, if any, of the age effect observed in my study. A longitudinal study of weight changes over individuals' lifetimes would be a good way to address this. Such data might come from sources such as Species360's ZIMS database (with the caveat that that accessing such data can be problematic, see: Section 2.4.3.1). Alternatively, reliable high quality data on body masses of various captive Prosimian species over several decades are freely available from the Duke Lemur Center's (Zehr et al., 2014). Such a study, given appropriate individual-specific weight and mortality data, could also determine i) if the current relative body mass threshold for obesity is appropriate; and ii) what effect time spent obese has on mortality. If the current threshold for obesity (>1.5) is appropriate, one would predict that obese animals would have shortened lifespans, especially those that reach this threshold from an earlier age (cf. Thorpe and Ferraro, 2004).

Females, but not males, differed seasonally in their relative body mass values, having larger values in the winter than in the summer and spring (Figure 6.5). Survey respondents indicated if female lemurs were pregnant, and I excluded known pregnant females from my analyses (see Section 6.2.1). However, pregnancy status might not always be known, and some of the females in my dataset could have been pregnant. Breeding is highly seasonal and often synchronised for wild lemurs (Wright, 1999). For instance, wild female ring-tailed lemurs in Bezà Mahafaly Special Reserve, Madagascar, come into oestrus (May/June) and are pregnant during the lean dry season, and give birth at the start of the more plentiful wet season (September/October) (Millette et al., 2015). Captive lemurs also maintain strongly seasonal breeding patterns, influenced by photoperiod and the latitude they are housed at (van Horn and Resko, 1977; Rasmussen, 1985). Thus, I cannot rule out that the females' seasonal pattern of relative body mass values might reflect pregnancies, emphasising the limitations of a purely observational study such as mine. Breeding is usually carefully managed in captivity, though, so an alternative explanation for the seasonal effect observed here might relate to a female's reproductive output being tightly linked with her body condition (Hume, 1995; Heldstab et al., 2017). Therefore, even if not pregnant, females of seasonal breeding species might nevertheless seasonally increase fat stores in preparation for the energetic expense of pregnancy and lactation (sensu 'capital breeding' Jönsson, 1997). Therefore, this result would indicate key times of the year during which females might be at increased risk of weight gain.

Limitations of this study include that my sampling method is non-random, as I focussed my recruitment on Species360 member zoos. Being affiliated with such an organisation may bring increased awareness of health and welfare problems of zoo-housed animals, and proactiveness in taking steps to improve conditions. Additionally, survey responses from so many different people likely introduces noise into my data (and see Section 2.4.3.2). As discussed in Chapter 5 unlike other indices of body condition, e.g. body mass index (NHS, 2019), relative body mass does not control for body length: important because this likely affects an individual's weight. Being observational rather than a controlled experimental study means that there may be other unmeasured variables that have not been considered here, e.g. calorie intake (sensu Selassie and Sinha, 2011), which could affect my outcome

and/or be confounded with my predictors. As described in Section 5.4.2, validation is now required to judge whether the current thresholds used here define overweight and obese animals are appropriate (i.e. 'obese' animals should be at increased risk of shortened lifespan, compromised reproduction and the diseases mentioned in Section 6.1). Nonetheless, these limitations aside, the nature of this type of study means that my results have predictive values as indicators of where problems arise from and how they may be addressed, this yielding directions for future research.

6.5 Conclusions

In this chapter I identified environmental and demographic risk factors associated with increased relative body masses, and implicit in this increased risk of being overweight or obese. Species were shown to differ in relative body mass values (ring-tailed lemurs and red-ruffed lemurs being largest), and this interacted with sex: female mongoose lemurs were heavier than males, but male ring-tailed lemurs were heavier than females. Female dominance and differences in species-specific perception of the captive environment could explain this finding. Relative body mass also increases with age, though it is yet unclear if increasing age *per se* is a risk factor for being overweight or obese. Provision of exercise opportunities affected males: those housed in enclosures featuring only fixed climbing structures had larger relative body masses than those housed with a mixture of flexible and fixed structures. Climbing structure provision appeared to have a strong effect on male relative body masses, as those housed with only fixed structures were on average obese. Based on this I recommend providing a mix of flexible and fixed climbing structures to encourage increased physical activity, and help prevent unwanted weight gain. Finally, for females there was an effect of season: females weighed in the winter had larger relative body masses than those weighed in the spring or summer. Being seasonal breeders, this finding might reflect unreported pregnancy. Alternatively, it could indicate that even if not pregnant, females seasonally gain condition in preparation for the energetic expense of pregnancy and lactation, emphasising certain times of the year they might be at increased risk of weight gain. Overall, my results emphasise both the complex, multifactorial nature of

weight and body condition across a population, and the benefits an approach such as this can provide in understanding health- and welfare-related outcomes.

Chapter 7: General discussion

As stated in Chapter 1, the main purpose of my thesis was to examine whether foraging niche has a predictive effect on welfare-relevant management problems within Carnivora, Psittaciformes, and Lemuriformes. For two groups, parrots (Chapter 4) and lemurs (Chapter 5), I found that foraging niche *did* predict their specific outcomes. Thus, in Chapter 4 reliance on wild food requiring extensive oral manipulation emerged as a biological risk factor for feather-damaging behaviour (FDB) prevalence across parrots. More tentatively, as the P value for this model was non-significant, in Chapter 5 I suggested a potential biological risk factor for increased susceptibility to captive weight gain across lemurs: "thrifty" adaptations associated with unpredictable wild food resources, as inferred from inter-year variation in annual rainfall within the native range. Contrastingly, none of the aspects of foraging niche examined in Chapter 3 were ultimately found to predict route-tracing across carnivores (reliance on self-hunted initially did, but this later disappeared once annual home range size was controlled for; Section 3.3.3). Leading on from my lemur comparative study, in Chapter 6 I also explored potential environmental and demographic risk factors for increased relative body mass across four species. Here, I confirmed that species differ in their relative body masses; found relative body mass to increase with age; uncovered opposing sex differences in two species; found females' relative body masses varied seasonally; and that males had larger relative body mass values when housed with only fixed climbing structures (as opposed to being housed with some flexible structures too).

Next, I briefly relate my findings to my five aims detailed in Chapter 1. In subsequent sections, I consider how my findings fit more broadly within the concept of animal welfare, then detail ideas for future research based on my work.

7.1 Relating my findings to my aims

I. Use phylogenetic comparative methods to identify biological risk factors for captive welfare-relevant management problems within Carnivora, Psittaciformes, and Lemuriformes.

As demonstrated in Chapters 4 and 5, I successfully used phylogenetic comparative methods to identify two biological risk factors for welfare-relevant outcomes in parrots and lemurs. I did not identify further biological risk factors for route-tracing across carnivores in Chapter 3.

II. Make tailored husbandry, housing, and enrichment recommendations based on successful identification of biological risk factors, hopefully to improve the wellbeing of thousands of individuals across different species.

In Chapter 4, based on FDB's biological risk factor I recommended that feeding naturalistic diets including the wild-type food, or suitable domesticated equivalent, such species would consume, e.g. shell-on tree nuts (Section 4.4.4). Additionally, because foraging enrichments have been demonstrated experimentally elsewhere to reduce the effects of FDB (Lumeij and Hommers, 2008), and are generally readily used and valued by captive animals (e.g. Markowitz and LaForse, 1987; Forthman et al., 1992; Shepherdson et al., 1993), I also recommended using these.

Regarding the potential biological risk factor for susceptibility to weight gain across lemurs (Chapter 5), most of my recommendations agreed with suggestions made elsewhere. My results complement these previous works by uniquely identifying which particular species – the "thriftier" ones – might benefit most from these because of their natural lifestyle. Thus, I agreed that care should be taken when designing captive diets to ensure animals, especially from the "thriftier" species, are not overfed calorie-rich diets (without restricting food *per se*) including commercial fruit (Goodchild and Schwitzer, 2008; Junge et al., 2009) (Section 5.4.1). I also agreed that increased exercise opportunities, and thus increased energy expenditure, should be encouraged (also see Taylor et al., 2012), e.g. flexible

climbing materials (also supported in Chapter 6 [Section 6.4]), and necessitating climbing and distances to be covered to access resources into enclosure design. Based on my results, to help reduce likelihood of captive food being signalled as being unpredictable (Sections 5.4 and 5.4.1), I suggested that zoos could consider giving animals, especially those from "thrifty" species, more frequent meals and/or *ad libitum* access to low-calorie food stuffs as a complementary or alternative method to feeding rations in discrete meals, e.g. including mature live trees within enclosure to provide browse. Doing so may reduce potential binge-eating and dominance effects at feeding times (see Sections 5.4 and 6.4), help reduce the likelihood of food availability being signalled as being unpredictable, and climbing trees to forage would also represent an exercise opportunity.

In Chapter 6, I was able to similarly make recommendations across four lemur species, but this time using epidemiology to identify an environmental risk factor for relatively large body masses. Thus, I recommended providing a mixture of flexible and fixed climbing opportunities as a feasible and easily implemented way to help address weight concerns. Based on demographic risk factors also identified in this chapter, I was also able to describe specific groups at increased risk of captive weight gain (e.g. male ring-tailed lemurs, *Lemur catta*, female mongoose lemurs, *Eulemur mongoz*, and perhaps older animals; Section 6.4).

III. Use findings to extrapolate beyond current datasets to predict how species new to captivity may respond; and/or suggest types of species currently within collections that might be also be predisposed to the problems examined here.

For parrots (Chapter 4), because of their relatively high reliance on wild food requiring extensive oral manipulation, i.e. FDB's biological risk factor (being a sole welfare indicator; see Section 7.2), I suggested the following species as being examples of those inherently less likely to be suitable as pets, e.g. yellow-tailed black cockatoos, *Calyptorhynchus funereus*, and blue-winged macaws, *Primolius maracana* (see Appendix 5 for values and further examples). In the upcoming Section 7.3 I also discuss that abnormal oral behaviours

performed by some carnivores might likewise be foraging-related, based on similarities in foraging behaviour between these species and parrots.

Implicit in my result in Chapter 5 is that the "thriftiness" enabling some lemur species to succeed in their unpredictably varied wild environments, renders the same species prone to weight gain under well-provisioned captive conditions. Therefore, one might predict that other taxa from similarly unpredictable wild environments may also be prone to weight gain in captivity.

Regarding Chapter 3, I did not have significant findings to base such recommendations on, so my predictions and suggestions were made based upon route-tracing's biological risk factor, annual home range size (Clubb and Mason 2003, 2007; Kroshko et al., 2016; with a similar trend in: Miller et al., 2018), and the pattern of route-tracing across species in my analyses. Thus, because route-tracing is predicted by large home ranges across Carnivora and by large daily travels distances across Primates (Pomerantz et al., 2013), a logical testable prediction is that, across taxa, being widely ranging predicts route-tracing. Additionally, as the three species with the most severe levels of route-tracing were all marine species (grey seals, *Halichoerus grypus*, harbour seals, *Phoca vitulina*, and polar bears, *Ursus maritimus*), I suggested that there may be something unique to marine species leaving them especially prone to time-consuming route-tracing (Section 3.4.1). Alternatively, as both the seals lacked annual home range size values this pattern could instead be explained by the home range effect, from which I would expect these species to also have relatively large annual home ranges.

IV. Use findings to assist in collection and population management decision-making, by suggesting species pre-adapted to be ill-suited to captive conditions.

Identification of biological risk factors aside, for all three of my comparative study chapters (3-5), there is a simple way for decision-makers to use the data in my thesis. Visually examining the phylogenetic tree figures from each chapter, with tip-points coloured

according to a given species' value, is a quick, easy way to judge at-risk species. Across carnivores (Figure 3.1), species most affected are grey seals and harbour seals (species-typical average time spent route-tracing by affected animals are 54 and 51%, respectively) and polar bears (30%). Likewise, examples of parrot species with most prevalent FDB (Figure 4.3) include Solomons cockatoos, *Cacatua ducorpsii* (67%), and Tanimbar cockatoos, *Cacatua goffiniana* (53%); while little corellas, *Cacatua sanguinea* (60%), Solomons cockatoos and monk parakeets, *Myiopsitta monachus* (both 50%) have especially prevalent other forms of stereotypic behaviour (SB). This information alone can help guide decisions about which species people managing captive wild animals should consider avoiding keeping (discussed in detail in Chapter 2). This point is a little different for lemurs, as being relatively large *per se* is not a welfare concern (although the associated health problems are; Section 1.2), meaning that zoos should not necessarily avoid keeping certain species based on their susceptibility to weight-gain alone. However, the lemur phylogenetic tree (Figure 5.3) highlights at-risk species: useful in targeting species requiring research attention to understand their large values.

As advocated in Chapter 2 and elsewhere (e.g. Clubb and Mason, 2003; Clubb and Mason, 2007; Müller et al., 2011; Pomerantz et al., 2013; McDonald Kinkaid, 2015; Kroshko et al., 2016) knowledge of biological risk factors themselves can directly inform collection management decisions. Therefore, because they are among those most reliant on wild food items requiring extensive oral manipulation in my dataset, at-risk species include the already mentioned Solomons cockatoos (FDB: 67%) but also white cockatoos, *Cacatua alba* (45%), salmon-crested cockatoos, *Cacatua moluccensis* (52%), and yellow-collared macaws, *Primolius auricollis* (50%). Thus, for the pet trade breeder and prospective owners might be encouraged to avoid keeping such species to avoid FDB.

V. Illustrate the strengths and weaknesses of using phylogenetic comparative methods in addressing animal welfare questions: a relatively novel research approach in this subject area.

The successful identification of two biological risk factors and the ability to make targeted recommendations based on them, illustrates the strength of this approach. Additionally, while causation (an issue I return to below) cannot be inferred from my results as analyses were only correlative (Gittleman, 1989), they do provide valuable direction for future research to establish this. My carnivore and lemur chapters in particular are good examples of how the comparative approach facilitates testing hypotheses that would be very difficult to address experimentally, e.g. do hunters need to hunt, and does "thriftiness" affect susceptibility to weight gain (sensu Chapter 2).

Weaknesses of this approach are mostly common to all comparative studies, although some are especially pertinent to welfare-relevant research questions. As for any study, the quality of comparative data is limited by the quality of the data contributing to them. To illustrate, the Captive Carnivore Database was particularly affected by missing values for husbandry data and some families were entirely unrepresented (Sections 3.2.1 and 3.4.1); some of the lemur species-typical wild mean body mass values came from single studies and few animals (Section 5.4); and I was unable to calculate the ideal predictor variables to test my FDB hypotheses (e.g. average % time spent handling food items; Section 4.2.2). As just mentioned, causation cannot be inferred from comparative analyses (Gittleman, 1989). To fully understand and address welfare problems causation must be addressed, and here the *results* of comparative analyses are useful as they inform direction for such research (see Section 4.4.1 for a detailed example of this regarding my FDB result). More specific to welfare-relevant research questions, is that outcomes are affected by *species*- and *individual*-level effects, and the statistics I used were not able to consider both simultaneously. As shown in Appendix 1, there are appropriate phylogenetically-informed statistical tests that *can* incorporate both effects (e.g. phylogenetic generalised linear mixed models: Hadfield, 2010). As all three of my comparative datasets had missing data for at some variables, such tests were inappropriate for my analyses, as using them would have

resulted in a large amount of data-loss. Nevertheless, as separating out phylogenetic and environmental effects statistically (cf. Hadfield, 2010) seems especially desirable for welfare-relevant outcomes, I would encourage future researchers to consider using such tests, and factor the need for a complete a dataset as possible into the study design stage.

7.2 My findings and animal welfare

In each chapter I focussed on a single welfare-relevant management problem, i.e. SB and susceptibility to weight gain. I did so because the nature of my research question and the hypotheses generated from it, but also for practical reasons (the carnivore and parrot datasets were readily available to me). The hypotheses I tested and risk factors subsequently identified are valuable, because they tell us something about the bases for those *specific* problems. However, my findings cannot be extrapolated to infer overall welfare. Because individuals and species (as evidenced in Chapters 3-6) vary in the way in which they respond to captivity and its challenges, to infer welfare in general one would need to use several welfare-sensitive indices (Broom, 1991; Mason and Mendl, 1993). The apparent lack of route-tracing by Pallas' cats, *Otocolobus manul,* may provide a relevant example here (Section 3.4.1). Inappropriately using route-tracing alone to infer welfare, one would say that animals from this species must therefore have relatively good welfare. This might indeed be true, but without assessing welfare more widely this cannot be confirmed. As discussed in Section 3.4.1, if some species, like perhaps Pallas' cats, are inclined to adopt alternative behaviours to SB under poor welfare conditions (e.g. inactivity associated with depression-like states, sensu: Fureix and Meagher, 2015; Fureix et al., 2016), then one would be incorrect in assuming that animals from species that do not route-trace have good welfare. Nevertheless, focussing on specific welfare-relevant management problems, as I have here, certainly provides welfare benefits to animals affected by them, and yields practical benefits to the people caring from them (cf. Section 1.2). However, as just discussed the absence of a problem should not be taken to equate to good welfare. Future researchers might therefore fruitfully examine biological risk factors for alternative welfare indices.

7.3 My findings and future research

As specific ideas for future research are discussed in detail within each chapter, here I attempt to draw out commonalties across relevant chapters in this final discussion on future research.

For my carnivore and parrot chapters (Chapter 3 and 4), their outcome variables are not directly comparable because of differences in their data collection and calculation. Because of literature-bias towards stereotypic animals, for my carnivore chapter the outcome was species-typical route-tracing severity of affected animals only (i.e. a sub-population of the overall population; see Section 3.2.2). Thus, calculation of overall population-level estimates, e.g. prevalence and population-level severity, was impossible (see also Section 2.4.3). Therefore, for most carnivore species the overall *extent* of this problem is unknown (but for studies on North American river otters, *Lontra canadensis*, and cheetahs, *Acinonyx jubatus*, respectively, see: Morabito and Bashaw, 2012; Quirke et al., 2012), but there are good estimates of how *severe* it is for the route-tracers. The opposite problem is found in the parrot dataset. Here, the sampling method used – surveying owners – did yield reliable estimates of population-level prevalence of a variety of SBs, but it does not produce reliable estimates of severity (see Section 2.4.3.2). So, the parrot dataset provides a good estimate of the *extent* of the problem across the population, but how *severely* animals and the population overall are affected is unknown. When it comes to assessing species-typical relative welfare, this point might be important. To illustrate, of the carnivores affected, grey seals and harbour seals spend the most time route-tracing and, of parrots, Solomons and Tanimbar cockatoos have the most prevalent FDB. But what if, say, only a few seals actually route-trace at all? Similarly, what if the cockatoos' FDB was very mild? One would likely draw different conclusions about relative welfare in each case if it was known there were species with as severe but more prevalent route-tracing, and those with as prevalent but more severe FDB. As it stands, this question cannot be addressed with the current datasets, and doing so by investigating how these metrics relate to one another and welfare could be very informative.

Remaining with my carnivore and parrot chapters, only for parrots did wild foraging niche have a predictive effect on SB. However, my carnivore chapter hypotheses and predictors only related to one form of SB – route-tracing – and the *food search* element (hunting) of the appetitive phase of foraging. In other words, food handling was not assessed in the carnivore chapter (and my parrot chapter also examined a more diverse range of SBs). In fact, on food search these two studies agreed: predictors relating to food search did *not* predict route-tracing across both (Sections 3.3.2 and 4.3.3). While route-tracing is the most common SB performed by captive carnivores (Mason et al., 2007), oral behaviours are also reported (e.g. bears, *Ursus* spp., and walrus, *Odobenus rosmarus*: Sergiel et al., 2014; Maślak et al., 2016; Fernandez and Timberlake, 2019). Therefore, future studies might examine whether restriction of the food handling element of wild foraging also predicts oral-related SBs in carnivores (see also Mason, 2006a) – and there may be some anecdotal support for this. Ocelots, *Leopardus pardalis*, pluck feathers from birds they catch prior to eating (Leyhausen, 1976; cited in: Murray and Gardner, 1997), so they, as some parrots do, likely have naturally extensive *food handling* behaviours. An ocelot that had been previously plucking hair from its own body, ceased when a more appropriate substrate was provided: whole unplucked bird carcasses (Hancocks, 1980). Another ocelot, when given a whole unplucked carcass for the first time, plucked all the feathers and then moved on to plucking the surrounding grass, to the extent the opportunity to pluck was described as "breaking the dam" (Morris, 1964; cited in: Hancocks, 1980). Some walruses repeatedly root and suck so much at the concrete surrounds of their enclosures that it wears their tusks down, risking infection (Mason, 2010), and oral attention can also be directed at their flippers (Hagenbeck, 1963; Fernandez and Timberlake, 2019). Walruses are molluscivorous, and these behaviours do resemble how they feed on mollusc beds in the wild (Mason, 2010). On this point, while observing parrots performing FDB is rare (Meehan et al., 2003b), when parrots are seen chewing/eating feathers, they reportedly pick the rachis apart seemingly to eat the pulp (Y. van Zeeland, pers. comm., 2016) – plausibly similar to the way in which they would naturally de-husk seeds and nuts prior to consuming the pulp (cf. Ullrey et al., 1991; Koutsos et al., 2001). Potentially, then, species whose natural foraging behaviour includes extensive oral food handling might be prone to oral SBs, especially perhaps those self-directed, resembling the food handling behaviour they would otherwise use. Regarding captive carnivores, there is a further research question relating to food handling. Soft, easily

processed captive diets requiring little food-handling, and/or which are nutritionally deficient, are proposed to lead to skull malformations and dental problems that affect some captive wild carnivores (and other mammalian species, reviewed by: O'Regan and Kitchener, 2005; Saragusty et al., 2014). In addition to oral SBs, then, prevalence of problems such as these might also be investigated in a carnivore comparative study (and potentially for parrots too). I would predict that species whose wild diets require extensive oral food handling behaviours would have higher prevalence of such problems.

One commonality that cropped up in both lemur chapters (5 and 6) is the, speculative, idea that the captive food environment might lead to signalling of food unpredictability. Unpredictability having been signalled could help explain a) the causal explanation underlying the potential biological risk factor uncovered in Chapter 5; and b) the sex effect observed in two species in Chapter 6. Thus, if feeding a small number of discrete meals rather than having food available *ad libitum* (Section 5.4), and/or if social hierarchy affects feeding priority and predictability (Section 6.4), then unpredictability could be signalled triggering associated behavioural and physiological mechanisms that in the wild are adaptive, but in captivity result in weight gain (cf. in humans: Nesse, 1984; Williams and Nesse, 1991; Mann et al., 2007; Pietiläinen et al., 2012; Nettle et al., 2017). Quantifying unpredictability having been signalled, however, would undoubtably be difficult, not least because the conservation status of lemurs (Schwitzer et al., 2013) rightly imposes limits on the nature of research involving them. However, if unpredictability *has* been signalled, then one would predict that affected animals should show readily quantifiable behavioural changes such as increased resting (cf. Wright, 1999). Finally, if food is presented in meals rather than being fed *ad libitum*, one would also predict that animals whose meals are fed on an unpredictable rather than predictable schedule should be relatively larger.

7.4 Final conclusions

In my thesis I found foraging niche did have a predictive effect on welfare-relevant management problems in parrots and lemurs. Thus, restriction of the food handling element

of appetitive foraging predicted prevalence of feather-damaging behaviour across parrots, formally identifying this as a biological risk factor. Conversely, restriction of behaviours relating to food search did not predict the stereotypic behaviour outcomes analysed here for both parrots and carnivores. Based on this, and taken along with some anecdotal evidence, I propose that investigating relationships between food handling and oral stereotypic behaviours, especially those self-directed, in carnivores is a logical next step. My results also support previous suggestions that certain forms of stereotypic behaviours likely reflect different motivational systems. For instance, I found feather-damaging behaviour to be distinct from other forms of stereotypic behaviours in parrots, including other oral forms; whereas these other forms of stereotypic behaviour both inter-relate with one another and share a biological risk factor (relatively large brain volumes). Additionally, the aspects of foraging niche examined in my carnivore study did not explain any of the variance in route-tracing not explained by annual home range size, with a similar effect found regarding other forms of stereotypic behaviours and relative brain volumes in parrots. For lemurs, "thrifty" adaptations to unpredictable wild food resources tends to render the same species prone to captive weight gain, and weight is also affected by demographic and environmental factors e.g. age and climbing structure provision within enclosures. Potentially, if captive food resources are being signalled as unpredictable, then this might help explain why some species, and individuals, are more susceptible to weight gain than others. Based directly on identified risk factors I made specific practical recommendations in each case, with potential to yield benefits to affected species and others, as well as providing direction for future research to better understand these specific problems. My findings may also have fundamental benefits to collection management and animal wellbeing across settings. That is, they should be incorporated into the decision-making process when deciding which species to maintain in zoos, and which are suitable as pets. As a tool for investigating the evolutionary basis for welfare-relevant problems of captive wild animals, I hope I have demonstrated the value phylogenetic comparative methods provide, with the ultimate aim of improving animal wellbeing.

Appendix 1

Reference table (Chapter 2) summarising some currently used PCM statistical tests (including software packages that facilitate these tests, with website links where appropriate).

Test	Preferred/required format of outcome variable	Preferred/required format of predictor variables	Comments
PICs Available in Mesquite (Maddison and Maddison, 2011): www.mesquiteproject.org/) using the PDAP:PDTREE module (Midford et al., 2010): www.mesquiteproject.org/pdap_mesquite/	Continuous with normally distributed residuals	Continuous, though can be adapted for categorical One predictor only	Relatively easy to use Good for poorly resolved trees, e.g. without branch length information, and/or with polytomies (Garland et al., 1992; Pagel, 1992) Easy to make simple modifications of the PIC procedure, e.g. apply different branch length transformations for different traits (Garland et al., 1992; Rezende et al., 2004), or assign branch lengths to be arbitrary or all equal if branch length information is missing (Grafen, 1989; Pagel, 1992) Robust to some violations of test assumptions (Garland et al., 1992)

R (R Team, 2015): www.r-project.org/ using the packages 'ape' (Paradis et al., 2004), 'caper' (Orme, 2013)	Typically does not incorporate non-Brownian Motion models of evolution (but see: Freckleton, 2012), but can partially correct for this by transforming branch lengths (Diaz-Uriarte and Garland, 1996; Garland et al., 1992)
	Possible to account for intra-specific variation in the Contrast program in PHYLIP (Felsenstein, 2008)
BayesTraits (Pagel and Meade, 2014): www.evolution.rdg.ac.uk/BayesTraits.html	Can therefore be too conservative, overcorrecting for this assumed strong signal (Diniz-Filho and Torres, 2002), so increasing Type II error
PHYLIP (Felsenstein, 2016): www.evolution.genetics.washington.edu/phylip.html	Creates non-intuitive graphs: contrast values are arbitrary (and can be biologically impossible negative values); contrasts can also be between an extant tip species and an estimated value for an ancestral node species, or between ancestral nodes, potentially even for historically impossible variables like ancestral enclosure size or IUCN status (correct, but non-intuitive)
Comparative analysis by independent contrasts (CAIC) for Macs (Purvis	

and Rambaut, 1995): http://www.bio.ic.ac.uk/evolve/software/caic/			Best for bivariate models; more complex models can be constructed using the contrast values from several individual models with the same outcome variable and different predictor variables (Garland et al., 2005), but this is time-consuming
PGLS Available in: R (R Team, 2015): www.r-project.org/ using the packages 'ape' (Paradis et al., 2004), 'caper' (Orme, 2013), 'phytools' (Revell, 2012), and 'Rphylopars' (Goolsby et al., 2016) BayesTraits (Pagel and Meade, 2014):	Continuous, though also performs well with pseudo-continuous ordinal (Graber, 2013), with normally distributed residuals	Continuous, categorical Multiple predictors	Can incorporate models of evolution aside from Brownian Motion (e.g. in 'ape': Paradis, 2011), such as Ornstein-Uhlenbeck and Early Burst (Harmon et al., 2010; Symonds and Blomberg, 2014) Thus weights for the phylogenetic signal that is actually present (Symonds and Blomberg, 2014), so not overly conservative For continuous variables can estimate intra-specific variation and measurement error using 'phytools' (Revell, 2012) or 'Rphylopars' (Goolsby et al., 2016), both in R (and based on Ives et al., 2007) Can easily use categorical predictor variables (Grafen, 1989)

www.evolution.rdg.ac.uk/BayesTraits.html			Intuitive graphs: species datapoints are plotted, with a PGLS regression line fitted (Symonds and Blomberg, 2014) Working with a poorly resolved phylogeny is possible (Symonds and Blomberg, 2014), but more difficult than PICs Need to use parameter estimates to obtain effect sizes and confidence intervals (Symonds and Blomberg, 2014)
Phylogenetic logistic regression Available in: R (R Team, 2015): www.r-project.org/ using the package 'phylolm' (Ho and Ané, 2014)	Binary (Ives and Garland, 2010)	Continuous, categorical (Ives and Garland, 2010) Multiple predictors	Gives an estimation of the strength of phylogenetic signal (Ives and Garland, 2010) Like PGLS, it weights according to signal present (performing as per standard logistic regression if there is no signal: Ives and Garland, 2010) Estimate of signal is only accurate if the binary outcome is relatively well balanced (i.e. similar number of 0s and 1s); otherwise performs poorly (Graber, 2013)

			Only models Ornstein-Uhlenbeck as standard (Ives and Garland, 2010) (but see: Ho and Ané, 2014)
Phylogenetic generalised estimating equations Available in: R (R Team, 2015): www.r-project.org/ using the package 'ape' (Paradis et al., 2004)	Continuous or discrete (counts or frequencies), normally or non-normally distributed (e.g., gamma or Poisson) (Paradis and Claude, 2002)	Continuous, categorical (Paradis and Claude, 2002) Multiple predictors (Paradis and Claude, 2002)	Good for non-normally distributed outcome data Particularly recommended for discrete data (counts or frequencies) (Paradis and Claude, 2002) The expected variance-covariance matrix structure is not really appropriate for binary data (Ives and Garland, 2010) Increased Type I error rates under certain circumstances (perhaps due to the degrees of freedom being an estimation of the true number) (Paradis and Claude, 2002) Does not give an estimation of phylogenetic signal (Graber, 2013)

Phylogenetic generalised linear mixed models (Bayesian inference using MCMC) Available in: R (R Team, 2015): www.r-project.org/ using the package 'MCMCglmm' (Hadfield, 2010) WinBugs (Lunn et al., 2000): www.mrc-bsu.cam.ac.uk/software/bugs/the-bugs-project-winbugs/	Continuous or discrete (counts or frequencies), normal and non-normally distributed, categorical, binary, ordinal Multiple outcomes (Hadfield, 2010)	Continuous, categorical Multiple predictors	Can separates out phylogenetic and environmental effects (Hadfield, 2010): potentially particularly interesting for zoo researchers Can incorporate measurement error (Hadfield & Nakagawa, 2010) (easier for outcome variables than predictors; Hadfield, J. pers. comm.) Useful for non-normal data (Hadfield, 2010) Bayesian inference is a very different philosophy from more common frequentist statistics; users may have to invest time familiarising themselves with this. Such differences include choosing sensible priors (though default ones are available) (Graber, 2013) For continuous data, only Brownian Motion is modelled (Martins et al., 2002) Analyses can be time-consuming (Hadfield, 2010)

Note that the R package is faster, and more user-friendly (Hadfield, 2010)			
Phylogenetic path analysis Available in: R (R Team, 2015): www.r-project.org/ using the package 'phylopath' (van der Bijl, 2017)	Continuous, with normally distributed residuals	Continuous, categorical Multiple predictors	Incorporates PGLS (to account for relatedness among species), into a model-testing procedure to unpick the most likely directional, causal relationships between predictors (Gonzalez-Voyer and von Hardenberg, 2014) Using standardised path coefficients, can compare the relative strength of each causal relationship in a model (Gonzalez-Voyer and von Hardenberg, 2014) Can incorporate various models of evolution(Gonzalez-Voyer and Von Hardenberg, 2014) If variables show strong collinearity, this can affect parameter estimation (Freckleton, 2011) and may reduce power (Gonzalez-Voyer and von Hardenberg, 2014). At lower levels, however, this method is an effective way to unravel collinearity between predictors (Gonzalez-Voyer and von Hardenberg, 2014)

	Slightly less power than non-phylogenetic path analyses, except under scenarios of strong signal; offset by decreased Type I error rates, even at weak levels of signal, compared to non-phylogenetic path analyses (Gonzalez-Voyer and von Hardenberg, 2014)
	Not yet possible to account for intra-specific variation (Gonzalez-Voyer and von Hardenberg, 2014)

Appendix 2

Table of errors found in the Kroshko et al. (2016) version of the Captive Carnivore Database, and how these were dealt with during the most recent update (see Section 3.2.2). SB=stereotypic behaviour. All SB=% observations that any form of SB is performed (not used in Chapter 3 as my focus was on route-tracing). SyMean_SyOnly%obs=mean % observations SB was performed by stereotyping animals. SyMean_All%obs=mean % observations SB was performed by all animals, including non-stereotypers (not used during analyses; see Section 3.2.2). Enclosure-level=mean SB performed by stereotyping animals within an enclosure (not used in analyses). Study mean=mean SB performed by stereotyping animals within a study (these means used in species medians calculations, see Section 3.2.2; see Table 3.3 for how this was dealt with for animals in multiple studies). Species median=species-typical median % observations route-tracing, i.e. my outcome variable in Chapter 3.

Study #	Individual # (name)	Species	Details	Comments
112	462 (Pele [2])	Jaguar	This animal was only 1 at the time of the study, i.e. a juvenile, and should be excluded from that study's calculations Multiple entries for him and for two other jaguars in this study (Tom and Inca, individual #s 460, 461)	Affects study mean. Across all jaguars it is 19.34% (was 19.92% previously).

Study #	Individual # (name)	Species	Details	Comments
142	550 (Shi Shi)	Giant panda	Suspect typo in previous database, meaning that Shi Shi's value for scratching was not included in 'All SB' calculations	Affects species median 'All SB': is now 2% (1% previously)
140	538 – 547	Giant panda	There was no 'SyMean_SyOnly%obs' value, even though there are individual-level SB data enabling this calculation	'All SB' value is 10%
154		Jaguarundi	No data on individuals provided (no individual #s, no information to explain why missing/incomplete)	No effect (as there was only a study SB value given for 'SyMean_All%obs' which is not used for analyses)
145		Leopard	Study sheet says 22 animals, but there is only individual-level data for 15	Affects species median, as the study mean should be 15.54% (for 15 animals; was reported previously as 14.33%)

Study #	Individual # (name)	Species	Details	Comments
			Old version had different values for 'SyMean_All%obs' and 'SyMean_SyOnly%obs', but as all pace it should be the same	
114, 115	463, 464, 465, 466	Lion	These are the same lions (Lumpy and Laura). Old version treated them as different lions rather than taking a study mean across these two studies. I therefore calculated a new study mean	Affected species median (my newly calculated study mean SB is 40%)
73	307	Margay	Exclude as 'young' and suspect juvenile	No effect on species median
68, 71, 72		Ocelot	Same individuals in multiple studies, thus need to calculate a study mean across all studies. However, it is unclear which individuals are in study #68. Study #68 has one animal from Chester Zoo (individual #289) which tallies with some of the animals in the other studies. But despite attempting various arrangements, I am unable to replicate the study mean calculation	Use Kroshko et al. (2016)'s value (19.62%)

Study #	Individual # (name)	Species	Details	Comments
I83		Snow leopard	Study mean should be 15.5%, which is different from the previously reported one (6.15%). Both animals stereotype, so unclear why the difference exists	No direct effect on species median, as other new studies were included in this version of the database
84	358, 353	Snow leopard	These are juveniles which were likely included in previous database calculations of enclosure-level mean SB calculations	No effect on species median as, being part of multiple studies, these animals were ultimately excluded from the study mean associated with them
9, 90		Tiger	These studies have five juveniles which should be excluded	No effect on study mean taken across studies. Does affect enclosure-level and study-level mean SB
87	374	Tiger	This animal is a juvenile. Is part of studies 87, 92, 93	Affects the study mean calculated across these studies, which is 13.87% (previously was 12.21%)
181		Tiger	Previously included two juveniles (660, 661) Some animals have missing individual-level SB data (individual #s 660, 662, 663) so assuming they did not stereotype. No value given for 'SyMean_SyOnly%obs' even though this should be calculatable using the individual-level SB data	No direct effect on species median, as other new studies were included in this version of the database

Study #	Individual # (name)	Species	Details	Comments
			available for individual #s 661, 664, 665, 666 and 667 Previous database version reported 5.38% for 'SyMean_All%obs' which I cannot replicate even *with* the juveniles. Correctly excluding the juveniles and assuming that the animals with missing individual-level SB data have 0% SB yields: 15.5% for 'SyMean_All%obs' and 23.25% for 'SyMean_SyOnly%obs'	
44	189, 190, 191	Meerkat	All three are juveniles. As a study mean only was reported in this study, this value is now unusable	Species now excluded from analyses (as this was the only meerkat study)
54, 55, 56	222 – 233	Eurasian lynx	These animals feature in all these studies, so a study mean taken across them all should be calculated. But despite attempting various arrangements, I am unable to replicate the study mean calculation	Affects species median. Study mean for 'SyMean_All%obs' is 4.14%, and as there was one animal that did not stereotype

Study #	Individual # (name)	Species	Details	Comments
				(individual #232), the 'SyMean_SyOnly%obs' should be 4.83% (previous version reported both as 3.47%)
177	657, 752	Neotropical river otter	This study's animals SB values were 26.3% and 14.09%, but the previous version had incorrectly reported the study mean as 26%	Affects species median. Study mean is 20.20%
125	497	Grey seal	This animal is missing individual-level SB data, so have assumed the value is 0%.	Affects species median. Study 'SyMean_All%obs' should be 62.58% and 'SyMean_SyOnly%obs' should be 69.53% (previous version reported 62.67% and 69.63% respectively)
	492, 493, 494		Previous version incorrectly reported enclosure-level mean SB for enclosure #403 to be 53.20%. The animals in that enclosure, stereotyped 19%, 72.4%, and 67.3% yielding an enclosure-level mean SB of 52.9%	
164	629, 630	Grey seal	These animals stereotyped for 30.55% and 45.35% yielding a mean of 37.95%, which was incorrectly reported in the previous version as 39.65%	Affects species median

Appendix 3

Table of species-typical median % observations (obs.) route-tracing values of 51 Carnivora species whose representatives' route-tracing status was known. N=number of individuals contributing to the species-typical median. Note that for species whose median route-tracing value is >0, representatives that did not route-trace were excluded from given sample sizes. Values shown in bold indicate the species featured in the final dataset for analyses. Values italicised indicate species with fewer than five route-tracing animals, thus excluding them from analyses. See Section 3.2.2 for details.

Species scientific name	Common name	Species-typical % obs. route-tracing	N
Acinonyx jubatus	Cheetah	**13.55**	**10**
Ailuropoda melanoleuca	Giant panda	*5.25*	*3*
Arctocephalus pusillus	Cape fur seal	0	2
Caracal caracal	Caracal	**14.75**	**10**
Catopuma temminckii	Asiatic golden cat	**23.56**	**5**
Cryptoprocta ferox	Fossa	**23**	**14**
Felis chaus	Jungle cat	*12.45*	*3*
Felis margarita	Sand cat	**12.68**	**9**
Felis nigripes	Black-footed cat	0	2
Felis silvestris	Wildcat	*1.5*	*2*
Genetta tigrina	Cape genet	*8.3*	*1*
Gulo gulo	Wolverine	*4.35*	*2*
Halichoerus grypus	Grey seal	**53.79**	**11**
Helarctos malayanus	Sun bear	**18.06**	**26**
Leopardus colocolo	Colocolo	*24.5*	*2*
Leopardus geoffroyi	Geoffroy's cat	**11.5**	**9**
Leopardus pardalis	Ocelot	**6.45**	**21**
Leopardus tigrinus	Oncilla cat	**11.5**	**8**
Leopardus wiedii	Margay	*12.49*	*4*
Leptailurus serval	Serval	**8.5**	**8**
Lontra canadensis	North American river otter	**5**	**6**
Lontra longicaudis	Neotropical otter	*15.88*	*2*
Lynx canadensis	Canadian lynx	**8.60**	**6**
Lynx lynx	Eurasian lynx	**10.83**	**10**
Martes flavigula	Yellow-throated marten	*7.7*	*2*
Melursus ursinus	Sloth bear	**15.49**	**5**

Nasua nasua	South American coati	*43.48*	*1*
Neophoca cinerea	Australian sea lion	*23.29*	*2*
Neovison vison	American mink	**8.95**	**7**
Odobenus rosmarus	Walrus	*51.27*	*4*
Otocolobus manul	Pallas' cat	0	7
Panthera leo	Lion	**6.25**	**10**
Panthera onca	Jaguar	**18.69**	**19**
Panthera pardus	Leopard	**9.38**	**35**
Panthera tigris	Tiger	**9.43**	**44**
Parahyaena brunnea	Brown hyaena	*24.7*	*1*
Phoca vitulina	Harbour seal	**51.15**	**10**
Potos flavus	Kinkajou	*57.2*	*1*
Prionailurus bengalensis	Leopard cat	*11*	*4*
Prionailurus viverrinus	Fishing cat	*9.17*	*3*
Puma concolor	Cougar	*11.75*	*3*
Puma yagouaroundi	Jaguarundi	*6.04*	*3*
Tremarctos ornatus	Spectacled bear	*39*	*3*
Uncia uncia	Snow leopard	**5.23**	**23**
Ursus americanus	American black bear	*14.95*	*3*
Ursus arctos	Brown bear	**19.68**	**44**
Ursus maritimus	Polar bear	**29.78**	**29**
Ursus thibetanus	Asiatic black bear	**7**	**25**
Vulpes lagopus	Arctic fox	**0.55**	**42**
Vulpes vulpes	Red fox	**0.16**	**11**
Vulpes zerda	Fennec fox	*9.68*	*4*

Appendix 4

Instructions for new Parrot Survey questions and other survey modifications, made to gain further information on the foraging environment of respondents' parrots for Chapter 4. Note, owing to technical problems, data resulting from responses to these questions were unusable (see Section 4.2.1)

Environmental enrichment (refers to pages 48-51 of the original Parrot Survey)

For question 1, edit slightly as follows:

1. For each of the enrichment opportunities mentioned below, please note whether you do/do not provide these to your parrot to keep it occupied:

a. Toys (*e.g.*, mirror, bell, plastic keys, etc.)
b. Foraging enrichments (*e.g.*, toys and puzzle feeders, scatter feeding/feeding from multiple locations, chewable/destructible materials, whole/larger food items, etc.)
c. Climbing and/or perching materials (perches, ropes, etc.)
d. Nest box
e. Hiding opportunities (*e.g.*, boxes, sleeping bags, etc., inside which the bird can hide)
f. Other, *i.e.* (with a box to fill in)

New question 2:

2. If you provide foraging enrichments to your parrot, what sort are they? Please check all that apply:

a. Toys and puzzle feeders, from which the parrot has to work to extract the food (*e.g.*, foraging tree, bird kong, treat wheel, etc.)
b. Scatter feeding or food fed in multiple locations (*i.e.*, food is scattered around for the parrot to find, or fed from several bowls around the cage or enclosure)
c. Whole or larger food items (*i.e.*, food is fed whole, not chopped or de-hulled, *e.g.*, whole walnuts, unshelled peanuts, Nutriberries, etc.)
d. Chewable and/or destructible materials (*e.g.*, rope, wood, etc.)
e. Irregular feeding times
f. Not applicable

The current question 2 becomes now becomes question 3, and is slightly edited as follows:

3. For each of the enrichment opportunities mentioned below, please note whether your parrot does or does not use it regularly (*i.e.*, at least once a day):

a. Toys (*e.g.*, mirror, bell, plastic keys, etc.)
b. Foraging enrichments (*e.g.*, toys and puzzle feeders, scatter feeding/feeding from multiple locations, chewable/destructible materials, whole/larger food items, etc.)
c. Climbing and/or perching materials (perches, ropes, etc.)
d. Nest box
e. Hiding opportunities (*e.g.*, boxes, sleeping bags, etc., inside which the bird can hide)
f. Other, *i.e.* (with a box to fill in)

The current question 3 becomes the new question 4. It is also edited slightly, and has the 'Foraging enrichment' option removed, so that the question looks like this:

4. If you offer toys (*e.g.*, mirror, bell, plastic keys) to your parrot, please note how many pieces you provide simultaneously:

And it has the current tick boxes to choose from (*i.e.*, 'not applicable', 'one at a time', 2-3 at a time'... etc)

A new question 5 is made as follows:

5. If you offer foraging enrichments to your parrot, for each of the options below please note how many pieces you provide simultaneously:

a. Toys and puzzle feeders, from which the parrot has to work to extract the food (*e.g.*, foraging tree, bird kong, treat wheel, etc.)
b. Whole or larger food items (*i.e.*, food is fed whole, not chopped or de-hulled, *e.g.*, whole walnuts, unshelled peanuts, Nutriberries, etc.)
c. Chewable and/or destructible materials (*e.g.*, rope, wood, etc.)

And it has the same tick boxes to choose from as the previous question (*i.e.* 'not applicable', 'one at a time', 2-3 at a time'... etc).

Make the current question 4 the new question 6, and edit it slightly as follows:

6. For each of the enrichment opportunities below, please note how you provide these to your parrot:

a. Toys (*e.g.*, mirror, bell, plastic keys, etc.)
b. Toys and puzzle feeders, from which the parrot has to work to extract the food (*e.g.*, foraging tree, bird kong, treat wheel, etc.)

c. Whole or larger food items (*i.e.*, food is fed whole, not chopped or de-hulled, e.g. whole walnuts, unshelled peanuts, Nutriberries, etc.)
d. Chewable and/or destructible materials (*e.g*., rope, wood, etc.)
e. Climbing and/or perching materials (perches, ropes, etc.)
f. Nest box
g. Hiding opportunities (*e.g*., boxes, sleeping bags etc., inside which the bird can hide)

Make the current question 5 the new question 7, and edit it slightly as follows:

7. With what do you fill/use for the foraging enrichments? Check all that apply:

a. Pellets
b. Seed mixture
c. Whole food items (*i.e.*, food is fed whole, not chopped or de-hulled, *e.g.* whole walnuts, unshelled peanuts, Nutriberries, etc.)
d. Not applicable
e. Other, *i.e*.(box to fill in)

Make a new question 8:

8. Are the items that you fill/use as foraging enrichment the entire daily ration for your parrot, or additional to its daily ration?

a. Entire ration
b. Additional to the daily ration
c. Not applicable

Make the current question 6 the new question 9, and edit as follows:

9. If you offer foraging enrichments to your parrot, how often do you do the following? Check all that apply:

a. Re(fill) toys and puzzle feeders, from which the parrot has to work to extract the food (*e.g.*, foraging tree, bird kong, treat wheel, etc.)
b. Scatter feed or feed in multiple locations (*i.e.*, food is scattered around for the parrot to find, or fed from several bowls around the cage or enclosure)
c. Feed whole or larger food items (*i.e.*, food is fed whole, not chopped or de-hulled, *e.g.*, whole walnuts, unshelled peanuts, Nutriberries, etc.)
d. Change chewable and/or destructible materials (*e.g.*, rope, wood, etc.)
e. Irregularly feed your parrot

And then have these options for each of the above categories as tick boxes:

- Not applicable
- Multiple times per day
- Once daily
- Once or multiple times per week, but less than once daily
- Less than once per week

Remove the current question 7 (How often do you replace the chewable items?) as covered in the new question 9.

Make the current question 8 (Which of the following kinds of climbing and perching materials are present...) the new question 10.

Make the current question 9 (Which of the following kinds of climbing and perching materials does your parrot use regularly...) the new question 11.

Make the current question 10 (How often do you rearrange the climbing materials?) the new question 12.

Make the current question 11 (At which time(s) of year do you provide the nest boxes?...) the new question 13.

Make the current question 12 (Please note how much time your parrot spends (on average) on interacting/playing with each of the below mentioned enrichment opportunities...) the new question 14 and edit slightly as follows:

14. Please note how much time your parrot spends (on average) on interacting/playing with each of the below mentioned enrichment opportunities:

a. Toys (*e.g.*, mirror, bell, plastic keys, etc.)
b. Foraging enrichments (*e.g.*, toys and puzzle feeders, scatter feeding/feeding from multiple locations, whole/larger food items, etc.)
c. Chewable/destructible materials (*e.g.* wood, rope, etc.)
d. Climbing and/or perching materials (perches, ropes, etc.)
e. Nest box
f. Hiding opportunities (*e.g.*, boxes, sleeping bags, etc., inside which the bird can hide)

Add in a new final question (15):

15. If you provide foraging enrichments to your parrot, please note how much time your parrot spends (on average) on interacting with each of the below. Please check all that apply:

a. Toys and puzzle feeders, from which the parrot has to work to extract the food (*e.g.*, foraging tree, bird kong, treat wheel, etc.)
b. Searching and eating food that has been scattered around the enclosure, feeding from food fed in multiple locations (*i.e.*, food is scattered around for the parrot to find, or fed from several bowls around the cage or enclosure)
c. Manipulating and consuming whole or larger food items (*i.e.*, food is fed whole, not chopped or de-hulled, *e.g.*, whole walnuts, unshelled peanuts, Nutriberries, etc.)
d. Not applicable

Nutrition (refers to pages 62 of the original Parrot Survey):

Make the current question 3 (Which of the following treats and snacks does your parrot regularly get? Check all that apply) the new question 2. Then make the current question 2 (How much do you feed your parrot?) the new question 3.

Make a new question 4:

4) How frequently do you refill/restock your parrot's food supply?

a. More than once per day
b. Once per day
c. Every second day
d. Twice per week
e. Once per week
f. Variably, dependent upon the percentage of food remaining. Please estimate the percentage of food remaining at which you refill/restock the food supply (with a box to fill in)

Make a new question 5:

5) Does your parrot regularly select certain items from its standard ration and leave others? If yes and you can identify these items, please give details:

a. Yes (with box to fill in)
b. No
c. Unknown

Make a new question 6:

6) Approximately how much, if any, of its standard ration does your parrot regularly not eat?

a. 0%
b. <10%
c. 11 – 25%
d. 26 – 50%
e. 51 – 75%
f. > 75%
g. Unknown

Make the current question 4 (On average, how many hours does your bird spend foraging and consuming food?) the new question 7

Medical history 3 (refers to pages 65 of the original Parrot Survey):

1) Has your parrot been diagnosed with any of the following medical problems? Check all that apply:
    a. None known
    b. Lipomas/ Xanthomas
    c. Atherosclerosis
    d. Liver lipidosis (fatty liver syndrome)
    e. Diabetes mellitus
    f. Pododermatitis (bumblefoot)
    g. Arthritis/joint problems
    h. Reproductive problems (e.g. reduced reproductive activity, egg binding)
    i. Hypothyroidism

Make the current question 1 (Does your bird have any diagnosed medical problems?...) the new question 2, and edit slightly as follows:

2) Does your bird have any other diagnosed medical problems? If yes, what are they?
    a. No
    b. Yes, *i.e.* (with a box to fill in)

Make the current question 2 (Do you give your parrot any medications?...) the new question 3.

Medical history 4 (NEW SECTION):

1) Please score your parrot's body condition using the guidelines below. Is your parrot:
    a. 1
    b. 2
    c. 3
    d. 4
    e. 5
    f. Unknown as I cannot handle my parrot

Appendix 5

Table of values for my two wild foraging predictor variables for all 200 of McDonald Kinkaid (2015)'s non-domesticated parrot species 'commonly kept in captivity', which formed the basis of Chapter 4. Species in bold are those with data from ≥ 5 birds for at least one outcome variable (see Section 4.2.1.1). RS=relative reliance on food requiring long search (%). RM=relative reliance on food requiring extensive oral manipulation (%)

Species name	Common name	RS (%)	RM (%)
Agapornis canus	Grey-headed Lovebird	50	0
Agapornis fischeri	**Fischer's Lovebird**	**20**	**0**
Agapornis lilianae	Lilian's Lovebird	30	0
Agapornis nigrigenis	Black-cheeked Lovebird	0	0
Agapornis personatus	**Yellow-collared Lovebird**	**0**	**0**
Agapornis pullarius	Red-headed Lovebird	30	0
Agapornis roseicollis	**Rosy-faced Lovebird**	**35**	**35**
Agapornis taranta	Black-winged Lovebird	100	50
Alipiopsitta xanthops	Yellow-faced Amazon	100	50
Alisterus amboinensis	Moluccan King-parrot	55	15
Alisterus chloropterus	Papuan King-parrot	100	50
Alisterus scapularis	Australian King-parrot	55	15
Amazona aestiva	**Blue-fronted Amazon**	**100**	**50**
Amazona albifrons	White-fronted Amazon	70	50
Amazona amazonica	**Orange-winged Amazon**	**100**	**0**
Amazona auropalliata	**Yellow-naped Amazon**	**70**	**30**
Amazona autumnalis	**Red-lored Amazon**	**100**	**0**
Amazona barbadensis	Yellow-shouldered Amazon	70	30
Amazona brasiliensis	Red-tailed Amazon	80	30
Amazona farinosa	**Mealy Amazon**	**80**	**30**
Amazona festiva	Festive Amazon	90	30
Amazona finschi	**Lilac-crowned Amazon**	**100**	**50**
Amazona guildingii	St Vincent Amazon	100	50
Amazona leucocephala	Cuban Amazon	70	30
Amazona ochrocephala	**Yellow-crowned Amazon**	**70**	**30**
Amazona oratrix	**Yellow-headed Amazon**	**70**	**30**
Amazona pretrei	Red-spectacled Amazon	100	20
Amazona rhodocorytha	Red-browed Amazon	100	0

Amazona tucumana	Tucuman Amazon	70	40
Amazona ventralis	Hispaniolan Amazon	100	50
Amazona versicolor	St Lucia Amazon	100	50
Amazona vinacea	Vinaceous Amazon	70	30
Amazona viridigenalis	Red-crowned Amazon	60	30
Amazona vittata	Puerto Rican Amazon	60	30
Anodorhynchus hyacinthinus	**Hyacinth Macaw**	**100**	**0**
Aprosmictus erythropterus	Red-winged Parrot	80	40
Ara ambiguus	Great Green Macaw	100	50
Ara ararauna	**Blue-and-yellow Macaw**	**70**	**30**
Ara chloropterus	**Red-and-green Macaw**	**70**	**30**
Ara glaucogularis	Blue-throated Macaw	100	0
Ara macao	**Scarlet Macaw**	**70**	**30**
Ara militaris	**Military Macaw**	**100**	**0**
Ara rubrogenys	**Red-fronted Macaw**	**50**	**40**
Ara severus	**Chestnut-fronted Macaw**	**80**	**50**
Aratinga acuticaudata	**Blue-crowned Parakeet**	**90**	**40**
Aratinga aurea	Peach-fronted Parakeet	60	30
Aratinga auricapillus	Golden-capped Parakeet	100	50
Aratinga canicularis	Orange-fronted Parakeet	100	50
Aratinga erythrogenys	Red-masked Parakeet	60	0
Aratinga holochlora	Green Parakeet	75	25
Aratinga jandaya	**Jandaya Parakeet**	**80**	**0**
Aratinga leucophthalma	White-eyed Parakeet	40	10
Aratinga mitrata	Mitred Parakeet	50	0
Aratinga pertinax	Brown-throated Parakeet	80	40
Aratinga solstitialis	**Sun Parakeet**	**100**	**0**
Aratinga wagleri	Scarlet-fronted Parakeet	0	0
Bolborhynchus lineola	**Barred Parakeet**	**70**	**30**
Bolborhynchus orbygnesius	Andean Parakeet	100	50
Brotogeris jugularis	Orange-chinned Parakeet	80	30
Brotogeris pyrrhoptera	Grey-cheeked Parakeet	60	30
Brotogeris tirica	Plain Parakeet	70	40
Brotogeris versicolurus	White-winged Parakeet	100	50
Cacatua alba	**White Cockatoo**	**100**	**100**
Cacatua ducorpsii	**Solomons Cockatoo**	**80**	**50**
Cacatua galerita	**Sulphur-crested Cockatoo**	**40**	**0**
Cacatua goffiniana	**Tanimbar Cockatoo**	**30**	**10**

Cacatua haematuropygia	Philippine Cockatoo	50	0
Cacatua leadbeateri	Major Mitchell's Cockatoo	20	20
Cacatua moluccensis	**Salmon-crested Cockatoo**	**100**	**50**
Cacatua ophthalmica	Blue-eyed Cockatoo	100	50
Cacatua roseicapilla	**Galah**	**0**	**0**
Cacatua sanguinea	**Little Corella**	**10**	**10**
Cacatua sulphurea	**Yellow-crested Cockatoo**	**100**	**50**
Cacatua tenuirostris	Long-billed Corella	0	0
Callocephalon fimbriatum	Gang-gang Cockatoo	100	60
Calyptorhynchus banksii	Red-tailed Black-cockatoo	100	50
Calyptorhynchus funereus	Yellow-tailed Black-cockatoo	100	100
Calyptorhynchus lathami	Glossy Black-cockatoo	100	100
Chalcopsitta atra	Black Lory	100	0
Chalcopsitta cardinalis	Cardinal Lory	100	0
Chalcopsitta duivenbodei	Brown Lory	100	0
Chalcopsitta sintillata	Yellow-streaked Lory	100	0
Charmosyna josefinae	Josephine's Lorikeet	60	0
Charmosyna papou	Papuan Lorikeet	60	10
Charmosyna placentis	Red-flanked Lorikeet	50	0
Charmosyna pulchella	Fairy Lorikeet	60	0
Coracopsis nigra	Black Parrot	80	20
Coracopsis vasa	Vasa Parrot	90	30
Cyanoliseus patagonus	Burrowing Parakeet	30	0
Cyanoramphus auriceps	Yellow-crowned Parakeet	35	35
Cyanoramphus novaezelandiae	Red-fronted Parakeet	40	10
Cyanoramphus unicolor	Antipodes Parakeet	10	0
Cyclopsitta diophthalma	Double-eyed Fig-parrot	80	30
Deroptyus accipitrinus	Red-fan Parrot	60	20
Diopsittaca nobilis	**Red-shouldered Macaw**	**100**	**50**
Eclectus roratus	**Eclectus Parrot**	**70**	**30**
Enicognathus ferrugineus	Austral Parakeet	45	15
Enicognathus leptorhynchus	Slender-billed Parakeet	45	15
Eos bornea	Red Lory	80	0
Eos cyanogenia	Black-winged Lory	80	0
Eos histrio	Red-and-blue Lory	100	0
Eos reticulata	Blue-streaked Lory	70	10
Eos squamata	Violet-necked Lory	60	0
Eunymphicus cornutus	Horned Parakeet	90	0

Forpus coelestis	**Pacific Parrotlet**	**50**	**0**
Forpus cyanopygius	Mexican Parrotlet	50	0
Forpus passerinus	**Green-rumped Parrotlet**	**30**	**0**
Forpus xanthops	Yellow-faced Parrotlet	50	20
Glossopsitta concinna	Musk Lorikeet	55	15
Glossopsitta porphyrocephala	Purple-crowned Lorikeet	100	0
Glossopsitta pusilla	Little Lorikeet	70	0
Guaruba guarouba	Golden Parakeet	70	10
Lathamus discolor	Swift Parrot	100	20
Loriculus galgulus	Blue-crowned Hanging-parrot	70	0
Loriculus philippensis	Philippine Hanging-parrot	70	0
Loriculus stigmatus	Sulawesi Hanging-parrot	70	0
Loriculus vernalis	Vernal Hanging-parrot	100	20
Lorius chlorocercus	Yellow-bibbed Lory	80	10
Lorius domicella	Purple-naped Lory	100	0
Lorius garrulus	Chattering Lory	100	0
Lorius lory	Black-capped Lory	100	30
Myiopsitta monachus	**Monk Parakeet**	**55**	**25**
Nandayus nenday	**Nanday Parakeet**	**60**	**30**
Neophema chrysogaster	Orange-bellied Parrot	0	0
Neophema chrysostoma	Blue-winged Parrot	0	0
Neophema elegans	Elegant Parrot	0	0
Neophema petrophila	Rock Parrot	0	0
Neophema pulchella	Turquoise Parrot	30	0
Neophema splendida	Scarlet-chested Parrot	0	0
Neopsephotus bourkii	Bourke's Parrot	0	0
Neopsittacus musschenbroekii	Yellow-billed Lorikeet	70	20
Nestor meridionalis	Kaka	70	20
Nestor notabilis	Kea	30	0
Northiella haematogaster	Blue Bonnet	40	10
Orthopsittaca manilata	Red-bellied Macaw	100	0
Phigys solitarius	Collared Lory	80	0
Pionites leucogaster	**White-bellied Parrot**	**100**	**60**
Pionites melanocephalus	**Black-headed Parrot**	**150**	**60**
Pionopsitta pileata	Pileated Parrot	70	30
Pionus chalcopterus	Bronze-winged Parrot	80	0
Pionus fuscus	Dusky Parrot	200	100
Pionus maximiliani	Scaly-headed Parrot	80	70

Pionus menstruus	**Blue-headed Parrot**	**70**	**40**
Pionus senilis	**White-crowned Parrot**	**100**	**50**
Platycercus adscitus	Pale-headed Rosella	50	20
Platycercus caledonicus	Green Rosella	60	40
Platycercus elegans	Crimson Rosella	60	30
Platycercus eximius	Eastern Rosella	60	30
Platycercus icterotis	Western Rosella	30	0
Platycercus venustus	Northern Rosella	80	60
Poicephalus cryptoxanthus	Brown-headed Parrot	70	40
Poicephalus gulielmi	**Red-fronted Parrot**	**70**	**40**
Poicephalus meyeri	**Meyer's Parrot**	**70**	**40**
Poicephalus robustus	Brown-necked Parrot	100	40
Poicephalus rueppellii	Rueppell's Parrot	65	25
Poicephalus rufiventris	**Red-bellied Parrot**	**100**	**50**
Poicephalus senegalus	**Senegal Parrot**	**70**	**30**
Polytelis alexandrae	Princess Parrot	50	50
Polytelis anthopeplus	Regent Parrot	50	20
Polytelis swainsonii	Superb Parrot	30	0
Primolius auricollis	**Yellow-collared Macaw**	**100**	**50**
Primolius maracana	Blue-winged Macaw	100	100
Probosciger aterrimus	Palm Cockatoo	70	30
Prosopeia tabuensis	Red Shining-parrot	100	10
Psephotus chrysopterygius	Golden-shouldered Parrot	0	0
Psephotus haematonotus	Red-rumped Parrot	40	10
Psephotus varius	Mulga Parrot	40	40
Pseudeos fuscata	Dusky Lory	80	0
Psittacula alexandri	Red-breasted Parakeet	70	0
Psittacula cyanocephala	Plum-headed Parakeet	90	10
Psittacula derbiana	Derbyan Parakeet	90	40
Psittacula eupatria	**Alexandrine Parakeet**	**70**	**10**
Psittacula krameri	**Rose-ringed Parakeet**	**70**	**10**
Psittacula longicauda	Long-tailed Parakeet	100	50
Psittacula roseata	Blossom-headed Parakeet	70	10
Psittaculirostris desmarestii	Large Fig-parrot	100	40
Psittaculirostris edwardsii	Edwards's Fig-parrot	100	0
Psittacus erithacus	**Grey Parrot**	**100**	**50**
Psitteuteles goldiei	Goldie's Lorikeet	100	0
Psitteuteles iris	Iris Lorikeet	100	0

Psitteuteles versicolor	Varied Lorikeet	100	0
Psittinus cyanurus	Blue-rumped Parrot	100	50
Psittrichas fulgidus	Pesquet's Parrot	80	0
Purpureicephalus spurius	Red-capped Parrot	60	50
Pyrrhura cruentata	Blue-throated Parakeet	100	50
Pyrrhura frontalis	**Maroon-bellied Parakeet**	**70**	**40**
Pyrrhura molinae	**Green-cheeked Parakeet**	**80**	**20**
Pyrrhura perlata	Crimson-bellied Parakeet	60	0
Pyrrhura picta	Painted Parakeet	70	20
Rhynchopsitta pachyrhyncha	Thick-billed Parrot	100	80
Tanygnathus lucionensis	Blue-naped Parrot	100	50
Tanygnathus megalorynchos	Great-billed Parrot	100	0
Trichoglossus chlorolepidotus	Scaly-breasted Lorikeet	90	0
Trichoglossus euteles	Olive-headed Lorikeet	100	0
Trichoglossus flavoviridis	Yellow-and-green Lorikeet	50	0
Trichoglossus haematodus	Rainbow Lorikeet	85	15
Trichoglossus johnstoniae	Mindanao Lorikeet	100	0
Trichoglossus ornatus	Ornate Lorikeet	100	0
Vini australis	Blue-crowned Lorikeet	100	0
Vini peruviana	Blue Lorikeet	90	0

Appendix 6

Lemur survey questions (yielding data used in Chapters 5 and 6)

Blurb: Previous research has found that some species of lemur are particularly prone to obesity in captivity, e.g. ring-tailed and blue-eyed black lemurs, yet others, such as greater bamboo lemurs and red-bellied lemurs, are not. We do not yet know, however, what the basis for these species differences in obesity-risk might be. Therefore, the purpose of this research project is to address why some lemur species are so much more obesity-prone than others. The main aim is to identify species-level 'risk factors' for obesity in captive lemurs, by uncovering relationships between species-typical ecological, dietary and biological traits and captive obesity-risk. Using these results, we will be able to better understand the basis for obesity, and manage and prevent it in the future. In order to accurately determine potential species-level risk factors, and statistically control for environmental factors that may also influence obesity, data on body weights, diet, and housing in captive adult lemurs are required. This survey has been designed to collect these data.

IMPORTANT: If you are happy to do so, to save time on some sections ZIMS Specimen reports and/or diet sheets can be provided, rather than completing those sections in full here. These sections will be clearly marked, and you will be asked to attach copies of ZIMS Specimen reports and/or diet sheets to an email. Additionally, there are spaces for up to 10 enclosures and 10 species to be described here. If you require more space than this, please email me and I can provide an alternative format: em15953@bristol.ac.uk

Please note that you may decline to participate and/or answer certain questions as you decide. All data will be treated as strictly confidential, and will be completely anonymised when written up. Once the project has been completed, a preliminary report will be sent out to all participants who provide contact details (approximately February 2018), as well as a later final report (approximately September 2018). This project and the survey have been granted ethical approval from Bristol University (reference number: 37201). If you have any questions about the survey or this project, please contact Emma Mellor: em15953@bristol.ac.uk

Thank you for taking the time to assist with this project!

Section 1: Basic information

Please note that throughout this survey unless specified we require information for ADULT lemurs only.

Name

Position held

Email address (please note that future project reports can only be sent if an email address is provided)

Name of zoo

Section 2: Enclosure 1

Which species of lemur is housed in Enclosure 1? Please choose one: *List option of all species of lemur currently held in captivity.*

How many adult males are there?

How many adult females are there?

How many sub-adults, juveniles and/or infants are there?

Enclosure and enrichment

Which option best describes this enclosure? *List options of: outdoor and indoor available all year round; outdoor available part of the year, indoor available all year; outdoor only; indoor only; prefer not to say; other*

Is the outdoor enclosure closed- or open-topped?

What are the approximate dimensions of the outdoor enclosure? Please give the length x width x height of the enclosure in meters. If the enclosure is open-topped please give the approximate height of the tallest tree/climbing structure:

Please indicate the types of climbing structures present in the outdoor enclosure. Check all that apply: *List options of: climbing structures that are rigid and fixed into place (e.g. platforms, bolted down logs); climbing structures that are unstable and flexible e.g. ropes, branches on a living tree; none; N/A*

What are the approximate dimensions of the indoor enclosure? Please give the length x width x height of the enclosure in meters:

Please indicate the types of climbing structures present in the indoor enclosure. Check all that apply: *List options of: climbing structures that are rigid and fixed into place (e.g. platforms, bolted down logs); climbing structures that are unstable and flexible e.g. ropes, branches on a living tree; none; N/A*

Which types and how often is environmental enrichment (EE), if any, usually offered in this enclosure? *Following options set out in rows, with columns with options to indicate the frequency for each*. Foraging EE (e.g. Kongs, feeding tubes, feeding puzzles, food placed into boxes); Manipulable EE (e.g. tyres, empty boxes, Christmas trees, toys [without food]); Olfactory EE (e.g. scents placed around the enclosure, essential oils, faeces from an unfamiliar animal); Sound/visual EE (e.g. radio, music or other sounds played, television); Training offered

Abnormal repetitive behaviours

For the purpose of this survey, abnormal repetitive behaviours (ARBs) are split into the following categories:

Category	Description
Self-injurious behaviours	ARBs that are directed towards the animal's own body with the potential to cause harm, including: self-biting; self-wounding; self-slapping; pulling/plucking at own hair; head-banging.
Self-directed behaviours	ARBS that are directed towards the animal's own body, but not directly causing harm. This includes: digit sucking, eye-covering, self-clasping.
Ingestive ARBs	ARBs that involve the animal consuming bodily excretions: regurgitation and re-ingestion; coprophagy (consuming faeces); urophagy (consuming urine). PLEASE SPECIFY FORM IN THE TABLE BELOW
Oral ARBs	Licking, chewing, and sucking non-nutritive objects, not directed at the animal's own body, e.g. cage/wire chewing or biting, bar gliding.
Locomotor (1) ARBs	Pacing and route-tracing: repetitively (at least three times without a break) following a set path or route within the enclosure. The route/path may include perches, walls, and branches.
Locomotor (2) ARBs	All other repetitive (at least three times without a break) locomotor ARBs aside from pacing and route-tracing. This includes: head-bobbing; twirling; somersaulting; hopping; back-flips; rocking; bouncing.

From the table above, how many of the adult lemurs of this species perform self-injurious behaviours? Please indicate 'none' if appropriate:

From the table above, how many of the adult lemurs of this species perform self-directed behaviours? Please indicate 'none' if appropriate:

From the table above, how many of the adult lemurs of this species perform ingestive ARBs? Please indicate 'none' if appropriate:

From the table above, how many of the adult lemurs of this species perform oral ARBs? Please indicate 'none' if appropriate:

From the table above, how many of the adult lemurs of this species perform locomotor (1) ARBs? Please indicate 'none' if appropriate:

From the table above, how many of the adult lemurs of this species perform locomotor (2) ARBs? Please indicate 'none' if appropriate:

Are there any other ARBs performed by this species that you wish to describe here?

Other enclosures

Do you have other lemur enclosures within your collection that you wish to describe here? *Yes/No answer. The participant's answer determines which questions they see next. If 'Yes' then the same set of enclosure questions as above appear (with space for up to 10 enclosures). If 'No' then they go on to the following section*

Section 3: Diet

To save time, if you are able to provide copies of diet sheets for the adult lemurs in your care, indicating if the amounts fed are per adult lemur or for the adults overall, please attach them in an email to: em15953@bristol.ac.uk

Please note that only information for adult lemurs is required.

Are you able to provide copies of diet sheets for the lemurs in your care? *Yes/No answer. The participant's answer determines which questions they see next. If 'Yes' they go on to the next section on body masses. If 'No' the following dietary questions appear*

Dietary information: Species 1

Which species is fed this diet? *List option of all species of lemur currently held in captivity.*

Please describe the typical diet fed to this species in grams per adult lemur per day. Please specify exact types (e.g. '100g apple, 50g lettuce' rather than '150g fruit and vegetables') and, where applicable, brand names:

How many times per day (including snacks) is this species typically fed?

Is there another species whose diet you wish to describe here? *Yes/No answer. The participant's answer determines which questions they see next. If 'Yes' the same dietary questions as above appear. If 'No' they go on to the next section on body masses.*

Section 4: Individual information

To save time, if you are able to provide copies of ZIMS Specimen reports for the adult lemurs in your care (including body masses and contraceptive status showing), please attach them in an email to: em15953@bristol.ac.uk

Please note that only information for adult lemurs is required.

Are you able to provide copies of ZIMS Specimen reports for the adult lemurs in your care? *Yes/No answer. The participant's answer determines which questions they see next. If 'Yes' they go on to the next section on body masses. If 'No' the following dietary questions appear*

Individual information: Species 1

Which species are you describing here? *List option of all species of lemur currently held in captivity.*

Are any of these animals currently given contraceptives or neutered (de-sexed)? *Yes/No/Prefer not to say. The participant's answer determines which questions they see next. If 'Yes' they see the first set of questions below, if 'No' they see the second, and if they answer 'Prefer not to say' they see the third.*

Body masses of Species 1 (*these are the 'Yes' questions*)

Body masses of animals who ARE currently given contraceptives / neutered (de-sexed)

For the adult males of this species, please give the weight, in grams (g), of each individual who IS currently given contraceptives / neutered (de-sexed, and the date (month/year) of weighing):

For the non-pregnant adult females of this species, please give the weight, in grams (g), of each individual who IS currently given contraceptives / neutered (de-sexed), and the date (month/year) of weighing:

Body masses of animals NOT currently given contraceptives / neutered (de-sexed)

For the adult males of this species, please give the weight, in grams (g), of each individual NOT currently given contraceptives / neutered (de-sexed), and the date (month/year) of weighing:

For the non-pregnant adult females of this species, please give the weight, in grams (g), of each individual NOT currently given contraceptives / neutered (de-sexed), and the date (month/year) of weighing:

For the pregnant adult females of this species, please give the weight, in grams (g), of each individual, and the date (month/year) of weighing:

Body masses of Species 1 (*these are the 'No' questions*)

For the adult males of this species, please give the weight, in grams (g), of each individual, and the date (month/year) of weighing:

For the non-pregnant adult females of this species, please give the weight, in grams (g), of each individual, and the date (month/year) of weighing:

For the pregnant adult females of this species, please give the weight, in grams (g), of each individual, and the date (month/year) of weighing:

Body masses of Species 1 (*these are the 'Prefer not to say' questions*)

For the adult males of this species, please give the weight, in grams (g), of each individual, and the date (month/year) of weighing:

For the non-pregnant adult females of this species, please give the weight, in grams (g), of each individual, and the date (month/year) of weighing:

For the pregnant adult females of this species, please give the weight, in grams (g), of each individual, and the date (month/year) of weighing:

At the end of each of these three subsections is this question:

Is there another species you wish to describe here? *Yes/No answer. The participant's answer determines which questions they see next. If 'Yes' the same individual information questions appear. If 'No' the following end of survey box appears*

Thank you for participating in this survey! If you are providing copies of diet sheets and/or ZIMS Specimen reports, please email them to: em15953@bristol.ac.uk

If you have any comments you would like to make, please use the space below:

Appendix 7

Cover letter to zoos requesting their participation in my lemur survey (Chapters 5 and 6)

To Whom it May Concern,

I am a PhD student from Bristol University in the UK, and part of my PhD is investigating species-level risk factors for obesity in captive lemurs. This project has support from the British and Irish Association of Zoos and Aquariums Research Committee, from the Association of Zoos and Aquariums' Prosimian Taxon Advisory Group Steering Committee, and has ethical approval from Bristol University (reference number: 37201).

I have designed an online survey to collect the data I require, and I wanted to ask whether ZOO NAME would be happy to participate, please (as I understand that you have lemurs in your collection)? The link to the survey is below, and ideally should be completed by someone working directly with the lemurs, or with access to their records (a keeper, registrar, or veterinarian), please:
https://goo.gl/forms/EEUNfqEH2p7mMsi22

Please note that you may decline to participate and/or answer certain questions as you decide. All data will be treated as strictly confidential, and will be completely anonymised upon writing up. Once the project has been completed, a preliminary report will be sent out to all participants who provide contact details (approximately February 2018), as well as a later final report (approximately September 2018). Additionally, my data collection period is due to on 31/12/17. If you would like to participate, I would politely ask that you do so before this date, please.

If you would like more information about the project or have any questions, please get in touch. I look forward to hearing from you.

Best wishes,

Emma

Appendix 8

Table of species-typical median relative body mass values for all 22 lemur species I had adult body mass data for. Note that those represented by fewer than five animals were excluded from analyses (see Section 5.2.1.2) and are italicised. Species with ≥ 5 animals but who used hibernation/torpor and related programmed fattening (sensu Dark, 2005; Fietz and Ganzhorn, 1999; Fietz and Dausmann, 2007), were also excluded from analyses (Section 5.2.1.2) and their values are underlined here. N=number of animals.

Species name	Common name	Species-typical median relative body mass	N
Cheirogaleus medius	Fat-tailed dwarf lemur	1.32	21
Daubentonia madagascariensis	Aye-aye	1.07	12
Eulemur albifrons	White-fronted lemur	*1.52*	*1*
Eulemur collaris	Red-collared lemur	1.11	17
Eulemur coronatus	Crowned lemur	1.28	21
Eulemur flavifrons	Blue-eyed black lemur	1.41	13
Eulemur fulvus	Brown lemur	1.53	11
Eulemur macaco	Black lemur	1.29	14
Eulemur mongoz	Mongoose lemur	1.16	29
Eulemur rubriventer	Red-bellied lemur	1.01	14
Eulemur rufifrons	Red-fronted brown lemur	*1.11*	*4*
Eulemur rufus	Red-fronted lemur	*1.26*	*1*
Eulemur sanfordi	Sanford's lemur	*1.10*	*1*
Hapalemur alaotrensis	Alaotran gentle lemur	0.97	12
Hapalemur griseus	Eastern lesser bamboo lemur	*1.48*	*3*
Lemur catta	Ring-tailed lemur	1.25	351
Microcebus murinus	Grey mouse lemur	1.24	44

Prolemur simus	Greater bamboo lemur	*1.04*	*3*
Propithecus coquereli	Coquerel's sifaka	1.08	17
Propithecus coronatus	Crowned sifaka	*1.11*	*3*
Varecia rubra	Red ruffed lemur	1.24	75
Varecia varigata	Black-and-white ruffed lemur	1.05	89

Appendix 9

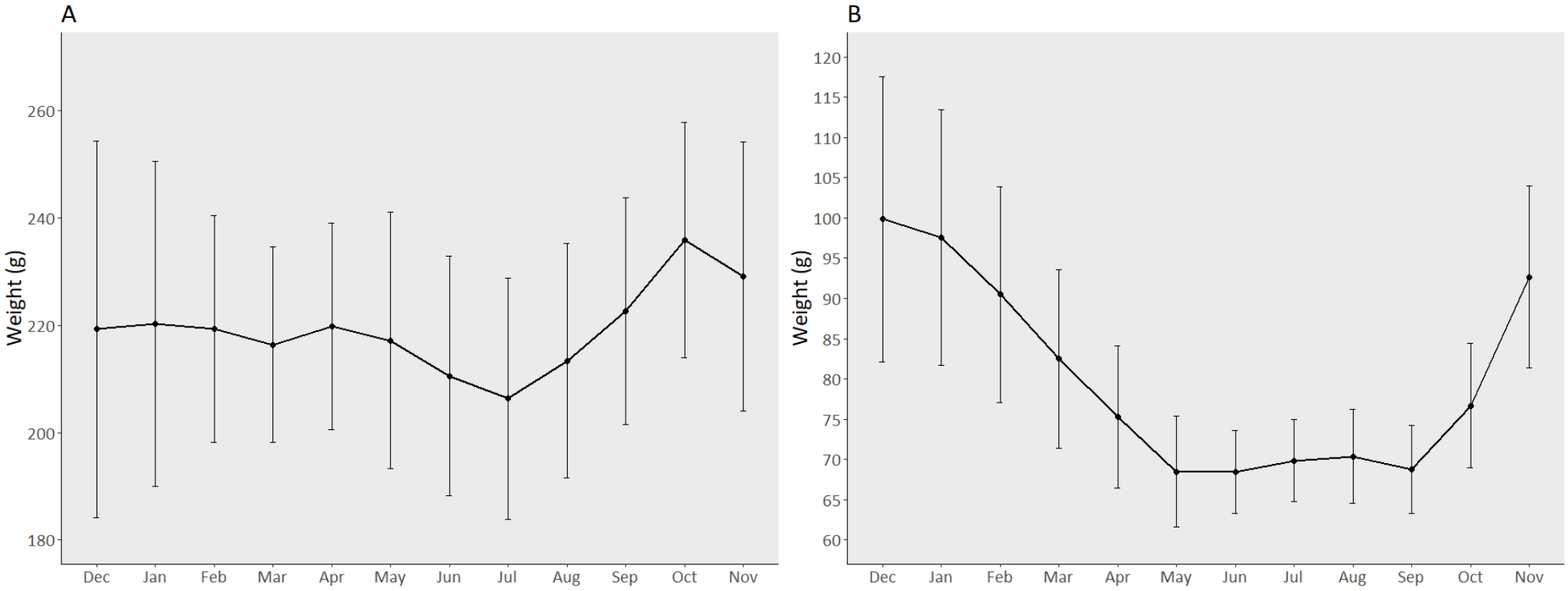

Figure showing patterns of seasonal weight-gain and loss in 21 captive fat-tailed dwarf lemurs (A) and 48 grey mouse lemurs (B) from one collection, taken over a 12-month period (December 2016-November 2017). Population means are plotted, and error bars show the standard deviation. Note that these lemurs are housed in the northern hemisphere, thus, their inactive period corresponds with winter in their captive environment. On Madagascar (southern hemisphere) this period is from May-October during the dry season (see Section 5.2.1.2 for rationale)

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